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Aphids as Vectors of Virus Diseases of Potatoes
A Literature Review

by Peter Langelüddeke

Editorial Note

In 1951, we published a literature review by Dr. R. von Rümker on potato degeneration. In the interim period, the importance of vectors has increased appreciably. Previously, a direct influence was attributed to very many factors which have now been found to be effective through the activities of the vectors.

Since the introduction of "E 605", we have concentrated our attention on the control of vectors. Progress in the protection of potato crops was not made, however, until more information had been gained on the habits of vectors and the epidemiology of leaf roll virus, in particular (cf. "Relations between infestation by vectors and spread of virus in potato fields", No. 5/1955), and until systemic insecticides were available. In beet farming, on the other hand, the control of vectors quickly led to a suppresion of yellows.

So much information is now available on the vectors, that this has developed into a most complicated subject. We have, therefore, decided to publish in the form of a literature review, extracts from a comprehensive paper on vectors, edited by the Phytopathological Institute of the Justus Liebig University in Giessen. This review should prove to be of valuable assistance to those engaged in the control of potato viruses, and to whom the different publications referred to here, are not accessible.

I. The transmission of virus by aphids (Mechanism of transmission)

Insects play a major part in the transmission of virus diseases. The ability to transmit viruses is, however, confined to a few orders of insects. According to Heinze (31), the most important of these is the Homopera order which includes bugs, cicadids, leafhoppers, aphids, scale insects etc. These are insects with piercing-sucking mouth parts, and their long sucking proboscis causes a deep puncture in the tissue although it does not destroy very many cells. Among the insects mentioned above, aphids are probably the chief vectors, According to Börner (8), there are approximately 830 aphid species in Central Europe alone, and of these about 80 are able to transmit plant viruses.

For most plant viruses, carrying by insects is the most effective or even the only method of transmission. The mechanism of transmission has, however,

not yet been completely clarified. Nevertheless it is certain that in most cases transmission is not purely mechanical otherwise it ought to be possible for highly infectious viruses like the tobacco mosaic virus or the X-virus of potatoes to be transmitted by insects. An exception to this is created by merely a few insects with chewing mouth parts such as grasshoppers and leaf-eating beetles. More important, on the other hand, is the normal "biological" transmission, in which certain relationships exist between insect, plant and virus.

Reproduction of the virus in the insect does not occur as a rule. Although reproduction of the virus of aster yellows has been proved to take place in its vector *Cicadula sexnotata* (Black, 1941), and is assumed for the virus of curly top of beta beet in *Piesma quadratum* (Völk and Krczal, 74), such cases are rare, and are not known for aphids.

Plant viruses capable of being transmitted by insects are considered as belonging to two general groups, a distinction being made between persistent and nonpersistent viruses.

Once having the ability, vectors of persistent viruses usually can transmit them to healthy plants for an extended period, often for life. But the vector is not able to infect healthy plants with the virus immediately after it has taken it in with food, and an interval is necessary before this can be effected. The length of this interval, the incubation period, varies for the different viruses and the vectors transmitting them. In fact, this period fluctuates between 20 minutes (beet curly top virus transmitted by beet leafhoppers) and 10 days or longer (e. g. potato leaf roll virus carried by green peach aphids). The incubation period may be explained as follows. The virus together with the plant sap taken in by the insect, enters the intestine, makes its way through the intestinal walls of the insect into the blood stream and thence into the salivary glands where it mixes with the saliva, and is then introduced with saliva back into the plant tissue during feeding. The virus of course takes a certain period to pass from the mouth of the insect into the intestine, and from here via the blood stream to the salivary glands, and the length of this period, at least in many cases, also depends upon the quantity of virus taken in. The more virus that is taken up, the earlier the vector will be capable of transmitting, and in consequence the incubation period will be proportionally shorter (Maramorosch, 46). During the translocation of the virus in the insect body, the intestinal wall appears to have a great bearing upon the suitability of the insect as a vector of the virus taken in. Storey (68) traced the virus in the intestine and blood of active insects, i. e. in those insects capable of transmitting the respective virus, but only found it in the intestine of inactive insects. The blood is apparently the main reservoir for the virus because it has only been traced in very small quantities in the salivary gland of numerous insects. However, when this gland begins to function, the concentration is raised, and apparently more virus is supplied from the blood only at irregular intervals. Therefore, it is only when the virus enters the salivary glands in adequate quantities while the insect is sucking on the plant that the plant can be infected, otherwise not at all. The longer the insect continues sucking, the greater will be the probability of the plant becoming infected.

In the group known as nonpersistent viruses, the insect carrier can transmit the virus immediately after feeding on a diseased plant. This ability of the vectors to cause new infections is soon lost, however. This group of viru-

ses can also be transmitted purely mechanically but practically speaking they rely chiefly on insects for transmission. Like the persistent viruses, they are not transmitted by purely mechanical means when carried by the insects. This has been proved in various tests in which nonpersistent viruses were to be transmitted by several aphid species having the same or a similar form of proboscis. The degree of infection caused in these tests varied appreciably. The procedure of transmission for these viruses still requires explanation. At all events, translocation in the insect body takes place quickly, because if it did not, a transmission soon after the virus is taken up by the insect would hardly be feasible. It is probable that the virus is drawn into the alimentary canal together with the food sucked by the insect, and ejected again when the insect makes its next puncture. Any virus left in the alimentary canal is presumably inactivated fairly quickly. It is quite likely that those viruses which cannot be transmitted by insects, such as the potato virus X, are merely a special form of nonpersistent viruses which are completely inactivated immediately they are taken in, or a few seconds later.

A peculiar feature is that a starvation period before feeding on infected plants usually increases the efficiency of vectors to transmit nonpersistent vectors, and sometimes transmission of these viruses is not possible until after the vectors have fasted. The effect of fasting was most perceptible after a brief period of sucking. Following a starvation period of several hours, Watson (77) allowed green peach aphids to feed for two to five minutes on plants infected with Hyoscyamus virus III, with the result that the transmission efficiency was greater than when the insects were permitted to suck on the plants for a longer period. These aphids remained capable of causing infection for 12 hours, but those which had not fasted beforehand were infective for only one hour. Watson presumed that a special substance is present in the aphid, which inactivates the virus, and which is all the more effective the longer the aphid feeds. But as a result of fasting, this substance is reduced in quantity, even though only temporarily, or rendered more or less ineffective. According to a recent theory put forward by Posnette and Robertson (57), there is always a certain quantity of inactivating substance present in the saliva, and this quantity increases when food is taken up, whereas it decreases as the result of fasting. The virus can be inactivated in definite quantities. When the virus is taken up in large quantities, the inactivating substance is not sufficient to be effective, and the virus accumulates in the insect. Later this process is reversed, and the insect loses its ability to cause infection. Important factors in this process are the concentration of the virus taken in by the insect, the rate of virus uptake during feeding, and the susceptibility or resistance of the virus involved to the inactivating substance.

Bawden (3) gives the following possible reasons for the fact that many viruses which can be transmitted by insects, cannot be transmitted mechanically:

1. The virus is present in the plant extract in too low a concentration.
2. It is inactivated too rapidly in the plant extract, whereas it remains active in the body of the insect.
3. Substances are present in the extract, which counteract the infection.
4. When transmitted mechanically, the virus does not enter the right tissue in which it can cause infection. This applies particularly to those viruses which are present in the phloem of their plant host, an example being the potato

leaf roll virus. In this case infection is caused only when the phloem is punctured, and this happens when the plant is attacked by aphids.

Many viruses, e. g. beet curly top, have only one vector, whereas others have several. Five or six aphid species are known to transmit potato leaf roll, and even more for other viruses. On the other hand, it is known that different strains belonging to the same kind of virus have different vectors. It is an established fact that two strains of potato yellow dwarf are transmitted by two different species of leafhoppers.

The vectors include a number which confine their transmission activities to one or a few viruses, and others which transmit a large number of diseases. The green peach aphid is known to transmit 75 viruses (Heinze, 31).

It is a strange fact that many viruses are only transmitted when the host also contains another certain kind of virus at the same time. The Aucuba virus of potatoes is only transmitted by the green peach aphid when virus A occurs at the same time in the infector plant involved.

II. The life-cycle of aphid species capable of transmitting potato viruses

1. The green peach aphid *(Myzus persicae* Sulzer) is outstanding amongst potato aphids, and is the most dangerous because it transmits with relative ease and certainty all potato virus diseases — with the exception of light mosaic — which are of economic significance in Central Europe.

a) Overwintering

Whereas the peach aphid occurs on almost 200 summer plant hosts, there are very few plants on which it can overwinter. Depending upon the prevailing winter climate, it overwinters in the egg stage on peach trees, or even in its summer form on outdoor winter hardies. The extent of overwintering in the different areas, in either the one or the other form, varies appreciably from year to year.

After fertilization, the wingless female lays six to eight eggs in autumn, depositing them singly or in groups mostly in the axils of the buds, between October and the middle of December. Apart from the peach *(Prunus persica),* the females also lay their eggs at times on apricots *(Prunus armeniaca)* and peach crossings. According to Hille Ris Lambers (36), Völk (70) and Gersdorf (24), overwintering and reproduction may also take place on a large scale on bird cherry *(Prunus serotina)* depending upon the occurrence of this host which is said to grow fairly frequently on light soils. Völk reports that the peach aphids which overwinter on *Prunus serotina* are of the same strain as those which spend the winter on the peach.

Heinze (30) writes in his paper that larvae emerging in spring are dependent upon the peach and apricot plants as hosts until the third ecdysis. It is not until they have almost grown to the adult stage that they are able to accustom themselves to other plants on which they reproduce later, e. g. when they fall from the peach tree and are then dependent upon weeds (Heinze and Profft, 34).

The number of eggs deposited per tree is said to vary. Heinze and Profft (33) counted in autumn 600 to 1000 females per tree, which had migrated back from the fields. These then produced oviparous females of which

each laid 6 to 8 eggs so that at least 4000 eggs were deposited, and probably many more. The above-mentioned authors discovered 15,000 to 20,000 eggs on large trees. Depending upon the location, however, these figures vary considerably. In the centre of large towns, for example, the trees are not so densely colonized as in the country. Furthermore, the density of colonization is also influenced by those factors which have a bearing upon the change in population density during summer and autumn, in particular the weather, attacks by parasites etc. These factors then determine the number of aphids migrating to peach trees in autumn.

Apart from the colonization density factor per tree, the number of trees growing per unit of area also has a great bearing upon the scale of the summer infestation to be expected in a certain district. This stand density varies most considerably in Germany, e. g. Heinze and Profft (34) quote 300 trees per 1000 hectares for Berlin and its immediate surroundings, and only 10 trees in the same unit area for Pomerania and East Prussia. In the latter two regions, the aphids migrating from these few host trees spread over a much larger area of potato fields than in the Berlin district. Furthermore, the aphids reproduce at a slower rate in parts of Eastern Germany because the vegetation period is later, and consequently the temperatures favouring reproduction also set in later on in the year.

The aphids are able to overwinter not only on peach trees but also in all possible protected places, exclusively in the form of virginogeniae. Not all the larvae which grow in autumn develop into sexuparae. Biologically, many resemble the summer winged aphids, while others remain wingless from the very outset (Heinze and Profft, 33). Many research workers (Börner et al.) presume that those aphids which overwinter in this form, belong to a special strain. This is disputed by Heinze and Profft (34), whereas Waldhauer (75 and 76), in a large series of tests he conducted, succeeded in proving that there are at least four groups of strains characterized by holocyclic or anholocyclic overwintering.

The following locations are of significance for anholocyclic overwintering:

1. Greenhouses to be found in towns and their vicinity, and also in villages, often in large numbers. Studies conducted in Lower Saxony by Heinze (30) revealed, however, that peach aphids do not overwinter in all greenhouses, whereas many other aphid species do. In many places in Germany, greenhouse overwintering is less important than overwintering on peach trees. In Holland, on the other hand, greenhouse overwintering is of importance because there are many greenhouses in that country. According to Björling (5), the same applies to Sweden where there are practically no other winter hosts of note, except in the South. In that country, especially in Schonen, there is said to be a high degree of conformity between the number of greenhouses and the rate at which *M. persicae* occurs in beet and potato fields. The peach aphid overwinters in greenhouses and also in winter gardens, mainly on Solanum varieties and tulips (Heinze, 30). Under favourable conditions, the progeny of a single aphid, developing in a greenhouse, can increase in numbers within three months to 2500 winged insects (Heinze, 32).

2. Aphids can be carried into cellars on cabbages and on beets which have also been properly stripped of their leaves, and also on flowers. They then occur on stored cabbage and germinating potatoes, sometimes in masses. It

occasionally happens that the few diseased tubers or infected aphids at first present in the cellar, cause complete infestation of the stock (Heinze and Profft, 33, and Moericke, 49).

3. Furthermore, aphids are able to overwinter in mangel, swede and fodder beet clamps, to which they are carried on the leaves of the plants stored there. At the end of the winter season or at the beginning of spring, the relatively high temperatures prevailing in these clamps constitute favourable conditions for a large-scale reproduction of the aphids so that such clamps often serve as the starting point for a dense and early aphid colonization.

In regions with a favourable climate, the peach aphid is also able to overwinter on certain plants outdoors. According to Heinze and Profft (34), this type of overwintering is only of importance in regions located west of the zero degree January isotherm and the line of the long-term January minimum of -11^{0} C. In Germany, these regions are confined to Schleswig-Holstein, parts of Lower Saxony and Westphalia, Rhineland and the plain of the Upper Rhine including the lower course of the Main.

Greatly varying temperatures have an unfavourable effect. The value of -9^{0} C given by Heinze and Profft (33), which insects are unable to tolerate for very long was, however, recorded in the laboratory. In nature, there are other factors besides the temperatures measured by meteorologists, which exert an influence. The temperatures in compact cabbage stands are frequently several degrees higher than in the air layer above where they fluctuate more appreciably than in the stand. Moericke (49) reports that following nine days of frost at temperatures ranging down to $-16{\cdot}5^{0}$ C during the winter of 1938/39, frozen aphids were found which, as the weather became warmer, revived and were also able to continue reproducing. Furthermore, snow blankets and wind shelters are occasionally of great significance (Heinze, 30, Hansen, 29). Another factor is the accumulation of water in the curled cabbage leaves (rainwater or melted snow), which can cause serious harm to the aphids sheltering there. The number of aphids overwintering in the field also depends upon the weather conditions prevailing in late autumn, in particular the temperatures in October and November, which have a relatively great bearing on aphid reproduction at this time of the year; furthermore, upon the time of the year when the cabbage is planted out. Cabbage planted in summer is more densely colonized than cabbage set in autumn (Steudel, 67).

Certain cabbage varieties, of which seed savoy cabbage is attacked the most heavily, are chiefly of importance with respect to overwintering in fields (Davies, 18, Steudel, 66, Haine, 26, and Rönnebeck, 62). Seed savoy cabbage is especially important because it is not harvested in spring until after the winged aphids have migrated. Brussels sprouts are also reported to suffer heavy colonization, although harvested earlier. According to Moericke (49), however, Brussels sprouts just like spinach and other cabbage varieties, are only slightly infested or not at all. Nevertheless, all these secondary hosts, also in Rhineland, are only of relatively minor importance. Rönnebeck (62) estimated several years ago that approximately 800,000 winged aphids developed in a stand of seed savoy cabbage merely a quarter of a hectare in size. On the other hand, he put down the number of migrants which developed from eggs laid on a peach tree at roughly 10,000 for moderate infestation, which suggests that in 1949 only half the number which occurred on moderately infested primary hosts, came from seed savoy cabbage. It is

reported that nowadays less savoy cabbage is grown than in 1949. This opinion on the major part played by primary hosts in the occurrence of alate aphids in spring was confirmed in respect of Rhineland by the results Martini (47) obtained in studies he conducted extending over a period of two years. Under conditions prevailing in Switzerland, Meier and Keller (48) also established that more than 90 % of the winged aphids occurring in spring originated from the peach. The same also applies to Holland (Hille Ris Lambers, 36).

In regions with milder climates, overwintering in the field appears to have a much greater influence. Davies (18) reports that in Wales, winter brassica crops, in particular savoy cabbage, supply the majority of the spring migrants. Broadbent and Heathcote (15) confirmed this view in that out of 238 winged aphids caught in spring, they could only determine two as fundatrigeniae. On the other hand, field overwintering in England, too, takes place only in mild winters (Doncaster and Gregory, 23). Hansen (29) discovered that in Denmark, green peach aphids occurred in the vicinity of marsh and other coast meadows in far greater numbers than in places some distance away, with the result that there was also a high rate of virus infection in the potato stands. Hansen presumed that the peach aphid is able to overwinter on certain perennial plants growing in these coast meadows but he did not give the names of these plants.

b) Development in spring

The eggs laid in autumn on the shoots of the primary host, chiefly in the axils of the buds, hatch in spring, and the fundatrix larvae emerge generally at the time when snowdrops are in bloom (Rönnebeck, 61). In Western Germany, the first larvae start to hatch out as a rule at the beginning of February, but not until the beginning of March in Central and Eastern Germany (Moericke, 49). According to Heinze and Profft (33), cold weather apparently has relatively little influence on the development of the fundatrix larvae which normally reach the adult stage within a few weeks. The same authors, however, discovered many dead larvae on buds following heavy rainfall, because these buds offered inadequate protection against adverse weather conditions. In 1949, Rönnebeck (61) recorded a relatively high mortality rate among both larvae and fully grown fundatrices, which was probably brought about by endogenous factors but not by predators or weather conditions. The percentage of eggs which hatched out was also very low, being estimated at 40 to 70 %.

The adult fundatrices produce agamic larvae soon after the final ecdysis, and these continue to develop into fundatrigeniae. Depending upon the climate and the year, up to three generations of fundatrigeniae are formed, and according to Heinze (32) winged aphids are produced by these in the third generation. When there are only two generations of fundatrigeniae, winged aphids are of course produced in the second generation. Rönnebeck (61), on the other hand, observed a number of winged aphids also in the first two generations, and these leave the peach host soon after the final ecdysis. Such aphids which fly from peach trees to summer hosts are termed as migrants. This means that migrants can be found among the direct offspring of the fundatrix. The development of the fundatrix from the time of hatching out until the

migration of the winged agamic females of the third generation of fundatrigeniae generally lasts from the beginning or middle of February until the end of May or the beginning of June. According to Rönnebeck, each fundatrix has between 500 and 2000 offspring when there are three generations. The earlier the fundatrix emerges and the more favourable are the weather conditions until the end of May, the greater will be the number of generations produced up to the time of migration. In consequence, there will also be more migrants.

Steudel (65) and Rönnebeck (61 and 63) have published the following dates for spring development (Rhineland). These correspond more or less to data given by other authors (Aue, 2, Moericke, 49, Koch, 41, Heinze and Profft, 33 and 34).

Steudel's data

Period of hatching out	1947 from March 31 onwards	1948 from Feb. 14 onwards
First flight of migrants	May 13	May 4—9
Commencement of winged summer aphid occurrence	June 20—24	June 10—15

Rönnebeck's data

Period of hatching out	1949 12. 2.—31. 3.	1950 10. 2.—15. 3.	1951 9. 2.—17. 3.	1952 middle of Feb.	1953 middle of Feb.
Oldest Fx fully grown on	1. 4.	29. 3.	10. 4.	10. 4.	2. 4.
Oldest Fg I fully grown on	17. 4.	18. 4.	30. 4.	21. 4.*	21. 4.
Commencement of peach blossom	6. 4.	3. 4.	7. 4.	—	—
First flight of migrants	6. 5.	6. 5.	10. 5.	28. 4.	3. 5.
Commencement of main flight	10. 5.	13. 5.	17. 5.	8. 5.	18. 5.
Heading of rye	6. 5.	15. 5.	19. 5.	10. 5.	17. 5.

* Period of hot weather between April 10 and 20.
Fx = fundatrix; Fg = fundatrigeniae.

Those aphids which have overwintered in the field, in greenhouses, clamps and cellars, migrate to the summer hosts during March or later, and fly firstly to various species of weeds because cultivated plants which make suitable summer hosts are not yet present in the fields at this time of the year (Moericke, 49). Naturally, the form and duration of overwintering are factors which also exert an influence on reproduction during this period before the aphids start migrating to the summer hosts (Steudel, 67). Dry, warm weather provides conditions more favourable for the development of the aphid population than damp cold weather, just as later on in summer. Those aphids overwintering in the field are of certain importance for the transmission of viruses among the respective winter hosts, and particularly on spinach according to Steudel. They cannot, however, transmit potato viruses from autumn until spring, but perhaps they become infective in spring when they colonize weeds which are also attacked by potato viruses. This of course is just as possible in the case of migrants flying from the peach hosts. It is only when infective aphids hibernate throughout the whole of the winter season — apparently this has never been observed to date — that they might prove dangerous (Heinze and Profft, 33).

c) Development in summer

The majority of the migrants start to fly from the peach trees in May, and this mass migration reaches its peak in the period following heading of the rye crop (Rönnebeck, 61 and 62). As soon as the rye begins to bloom, most of the aphids have already left their winter hosts.

The majority of the winged agamic females generally begin to migrate from the peach trees four to seven days after the first winged aphids have developed. The main flight period usually lasts two to three weeks, so that this period reaches its peak 11 to 18 days after the departure of the first migrants. This main flight period, however, always precedes the development of the first winged virginogeniae, so that the time and strength of the migrant flight are the main factors which have a bearing upon the colonization of the summer hosts (Rönnebeck, 62). By the middle to the end of June, all the aphids have flown away from the peach trees, or else they have perished (Heinze, 32). Doncaster and Gregory (23) report that in England, following migration from the peach trees, there is also the possibility of yet another large batch of aphids flying to summer hosts from cabbage plants on which they have spent the winter.

Provided they have already emerged, the potatoes will be colonized by the first groups of migrants flying from the peach trees. Potatoes are the chief summer plant hosts of the green peach aphid which thrives best on this crop. But in addition there are very many other plants from a wide variety of families, cultivated plants and weeds alike, which are colonized by this pest. Börner (8) states that there are more than 200 different kinds. The potatoes often emerge relatively late depending upon when they are planted out, with the result that they are not always colonized by aphids flying direct from the winter hosts. Often, the aphids fly to the potato fields from other plant species which they attack first, or even from potato fields where the crop has emerged earlier and where the aphids may already have become infective.

According to Moericke (49) a distinction is made between two forms of flights both for migrants as well as for virginogeniae, these being known as

the swarm flight and the colonizing flight. Very soon after it casts off its final larval skin, the winged aphid becomes active and flies off, even when it is on a plant where it could reproduce. This swarm flight can of course be stemmed by the wind but not prevented (Haine, 28). The wind only has to drop for a few seconds — brief periods of calmness can always be reckoned with particularly close to the ground — and the flight can start. Apparently it is not affected even by high relative humidity. After leaving their hosts, the aphids immediately rise straight up into the air — or if not at once, then a short distance away from their starting point — and then fly more or less actively with the wind. After flying off, the aphids may become caught in strong upwinds or horizontal air currents so that they drift passively at great altitudes, and are carried over long distances. When the weather is absolutely calm, the direction of flight is indefinite, and it is most likely that a certain stimulus of light has an influential effect. According to Müller (55) the insects always fly against the wind when it is not blowing strongly. Gradually, the aphids display a tendency to attack the plants, perhaps after they have been flying for a certain period and, provided the prevailing air currents permit, they attempt to land in the fields.

All other flights of a colonizing or marked attacking nature, proceed over relatively short distances, being very greatly influenced by the prevailing weather conditions, i. e. by temperature, relative humidity and wind force. To recapitulate, the aphids are transported over long distances in swarm flights — provided they have developed on infected plants, they are, therefore, able to carry virus diseases also to remote areas — whereas in the following period, the so-called colonization phase, they fly from one plant to the other where they feed and produce offspring. The length of time spent by the aphids on the different plants depends upon the prevailing weather. These frequent "trial" flights from one plant to the next have particular bearing upon the transmission of virus within a stand, that is when nonpersistent viruses are carried.

Previously it was believed that the aphids are able to find their plant hosts mainly with the aid of their sense of smell (Profft, cited in 49), but studies conducted by Moericke (49 and 52), particularly in tests where this author made use of trap vessels, revealed that, in the main, light and colour attractions, particularly yellow and light-green colours, cause the green peach aphid to land. During flights when they are carried with the wind, the aphids cannot pick out suitable plants quickly enough by means of their sense of smell, this being the reason why they are often found also on plants which do not belong to the host category. Whenever the aphids suddenly develop an urge to attack plants while they are in flight, they settle on any areas which attract them because of the colours, and make punctures in the attacked plants to try them out for their suitability as hosts. When the taste test shows that the respective plant is after all a suitable host, the aphid crawls on to the lower surface of the leaf, and if not it flies away in search of another place where it can obtain food. Whether the aphid does actually continue its flight or remains on a plant which is possibly less tasty, also depends upon the inclination it still has to fly, its degree of exhaustion, or its hunger. Once the aphid has dropped to the ground, contact stimulus and the attraction of sweet smells may also influence its selection of plant hosts. Müller (53) believed

he had established that *Doralis fabae* displays a certain ability to select plants while it is in flight due to its sense of smell, but later (54) he confirmed the results obtained by Moericke in his studies.

The insects of the first generation produced by migrants on potatoes, are always apterous. The next winged aphids are not produced until during the second generation, some four to five weeks after the first migration, and hardly before the middle of June (Heinze, 32). In fact, these winged aphids do not develop in large numbers until after the beginning of July. The larvae take about a fortnight to reach the adult stage at temperatures of 18 to 20° C. The rate at which they grow and continue to reproduce, depends mainly upon the temperature. According to Heinze and Profft (34), the most favourable temperature is between 22 and 24° C whereas at temperatures above 30 to 32° C no further reproduction takes place, and the aphids die off in large numbers as a result of the heat. The peak of infestation is generally reached during July, but after a particularly warm and dry early summer it may even be reached in June. Davies (18) states that when the summer is exceptionally cold this peak is not reached until August. The extent of aphid colonization also varies from year to year, and from place to place. Only a very small percentage of all aphid species ever develops into winged insects.

Once the aphid population has developed to maximum strength, as a rule in July, it often collapses completely within the space of a few days so that frequently no more aphids are to be found. There are various reasons for this. Doncaster and Gregory (23) are of the opinion that when infestation is heavy or very heavy, nearly all the growing larvae develop into winged aphids and migrate. When the infestation is weaker, the percentage of winged aphids is said to be less and the drop in infestation is a correspondingly slower process; furthermore, those aphids which migrate are believed to remain on other plants, e. g. cabbage species, until autumn. According to many other authors, predators of aphids may also occur on a more or less large scale thus bringing about the drop in infestation. Unfavourable weather, e. g. heavy downpours of rain, may also contribute largely to a decrease in the infestation density, although not being the direct cause of it.

d) Development in autumn

An important feature of development in autumn is that in contrast to the summer development, it also takes place to a much greater extent on plants other than potatoes because many of the potato fields have already been harvested. Presumably under the influence of temperature and the length of the days, or the food conditions, winged gynoparae develop from the middle to the end of September until the beginning of October (Heinze and Profft, 33), or until well into November (Moericke, 49). Some time later the winged males develop, and these are considerably outnumbered by the gynoparae. Moericke (50) also observed the occurrence of winged virginoparous aphids (virginogeniae), particularly on cabbage; these were in the majority on beets but here the percentage of males and winged gynoparae was appreciably greater, whereas on potatoes and tomatoes hardly any virginogeniae but mainly gynoparae developed. Moericke assumed that these phenomena are due to the influence of food conditions, and possibly also to the presence of two strains, one

holocyclic and the other anholocyclic. In fact, this has been confirmed in the meantime by Waldhauer (75 and 76). From the end of September onwards, gynoparae fly to the peach trees, followed later by the males. According to Broadbent (10), they find their winter hosts purely by chance because they, just like ther mates, are unable to detect the hosts with their organ of smell. The egg-laying (oviparae) females are produced by the gynoparae on the peach trees, and on reaching the adult stage (middle to end of October), they are copulated by the males. From the end of October onwards, the females then lay their eggs on the peach trees or on the other winter hosts, mainly in the axil between the bud and branch, and also in cracked bark (Heinze, 32).

2. *Rhopalomyzus* or *Myzus ascalonicus* Donc. occurs on numerous plants, shows no particular liking for either potatoes or beets, but transmits viruses from both. It apparently overwinters only in the virginogenous form. This species is easily mistaken for *M. persicae*.

3. *Neomyzus circumflexus* Buckton frequents greenhouses, and also occurs in the field. No cases of mass infestation have been observed to date. This species transmits potato and beet viruses.

4. *Myzus ornatus* Laing is less widely spread than no. 3. It can only overwinter in greenhouses because it perishes in the field during the winter season. It occurs only in the summer form, colonizes many species of plants, and is capable of transmitting streak and leaf roll virus.

5. *Aulacorthum* or *Dysaulacorthum pseudosolani* Theob. transmits viruses on relatively few occasions. Its chief plant host is the potato, and at times beets are also colonized. The eggs are laid indiscriminately, also on dead material, in autumn. The aphid overwinters in cellars, greenhouses etc. When it punctures the plant, it causes serious damage to the tissue due to the injection of saliva, and therefore it has difficulty in transmitting virus diseases. Punctures made in the conducting strands are most likely to lead to an infection, because here the virus can be translocated away quickly from the directly damaged tissue.

6. *Macrosiphon solanifolii* Ashm. is encountered more frequently than the aforementioned species, particularly in the warmer regions of South and South-West Germany where it is better able to overwinter and reproduce. It occurs on potatoes later and in fewer numbers than *M. persicae*. It is to be found quite often in the vicinity of villages. This species overwinters on germinating potatoes in cellars, and on ornamentals in greenhouses. Oviposition has not been observed to date. The green potato aphid is capable of transmitting streak virus, possibly leaf roll virus, and also beet viruses.

7. The buckthorn aphid (*Doralina transiens* Walk.) occurs chiefly on potatoes, sometimes in far greater numbers than the green peach aphid. Its main winter hosts are buckthorn (*Rhamnus carthatica* and *Rhamnus alnifolia*), also *Rh. infectoria* and *Rh. saxatalis* which are widely spread. The buckthorn aphid overwinters only in the egg stage. The fundatrix emerges at the beginning of April; migrants develop in the second generation of fundatrigeniae, and they colonize the potatoes later and with more hesitance than the green peach aphid. In good weather conditions, the buckthorn aphid may occur in masses, with relatively little difference between degeneration and non-degeneration areas. In 1937, Heinze and Profft counted 900 buckthorn aphids per plant in Dramburg, and 4300 per plant in Dahlem. Comparison figures for

M. persicae: 25—30 and 5400, respectively. In healthy districts, this pest often occurs far more abundantly than the green peach aphid, but as a vector it is a most sedentary insect. It definitely transmits Y-virus but whether it also carries leaf roll and beet viruses is still a controversial question.

III. The influence of environmental conditions upon change in population density and infection by virus diseases

1. The influence of temperature

Temperature has the greatest influence of all climatic factors — mostly the influence of these factors cannot be sub-divided — upon aphids, in that reproduction is fully dependent upon it. The first indication of this influence is in early spring when hatching begins, this process taking place between the beginning of February and the middle of March depending upon the prevailing weather. In the following period, the development of the generations of fundatrices and fundatrigeniae, and the size of these generations depend upon the prevailing temperatures. According to Moericke (49), high temperatures and dry conditions greatly stimulate development during this period. This in turn determines the number of migrants flying from the peach trees; these migrants are the progenitors of virus-transmitting summer generations. The effect of the temperature upon the life-cycle of such a generation and the number of offspring is indicated by the following figures:

According to De Jong (cited in 49), the results of laboratory tests gave a life-cycle of 18 to 20 days at 24·5° C, and 55 to 65 offspring. At 28° C, only 19 offspring are produced per parent insect because it does not live so long at this temperature. At 30° C, the larvae produced do not develop to the adult stage. Weed (cited in 49) quotes 45 offspring per aphid at 10° C. These figures also agree with those published by Heinze and Profft (34) who give 22 to 24° C as the best temperature range for reproduction, stating that at temperatures above 30° C no further reproduction takes place.

The fact that temperatures not only influence reproduction but also the activity of the aphids is illustrated by the laboratory tests of Davies (19) who counted the number of flights per minute for a certain number of winged *M. persicae* with variation of temperature and relative humidity. At 12·8° C (= 55° F), there was very slight flying activity, whereas at 26·6° C this activity was greatest. At all events, the flying activity was greater at low relative humidity, becoming less as the relative humidity increased, and ceased completely at 100 %. But even then, the aphids were still rather mobile particularly when the temperatures were high.

2. The influence of relative humidity and rainfall

It is difficult to say what influence relative humidity has upon aphid reproduction because low relative humidity is mostly coupled with high temperatures, and vice-versa. According to Heinze and Profft (34), inter alia, its direct influence, however, is apparently relatively slight because the aphids, due to their sucking habits, are almost independent of the moisture content of the air. Hansen (29) ascribes a certain degree of importance to relative humidity because the microclimate in a plant stand is very greatly dependent upon it. Even when the relative humidity drops again following rainfall, it still

remains in the region of 100 % in the stand itself as long as the leaves and the soil are still wet. Furthermore, there may also be an increased formation of dew at high relative humidity and low night temperatures, causing serious harm to the aphids especially when a considerable amount of dew is formed for several consecutive days (Heinze and Profft). But it is uncertain whether the condensation water causes direct harm to the aphid organism or whether the occurrence of fungal diseases is stimulated.

In general, a certain harmful effect exerted by rainfall is established by many authors. Long persistent periods of rainfall and sudden downpours may have a particularly unfavourable effect upon the aphids because they may be washed away when they are not concealed in sheltered places, or hit by dirt splashes which render them inactive. However, the aphids are always to be found on the lower surface of the leaves — with few exceptions — where they are afforded good protection also against heavy rain, especially when the leaves have curled due to injuries caused by the aphids feeding on them. This protection, however, is not so effective on plant species or varieties with rather upright leaves, and on plants infected by leaf roll when the leaves curl upwards. Not all rainfall, in particular general rain, need have any effect upon the aphids. It has in fact often been observed that colonization has increased despite a large amount of rain (Heinze and Profft, 34, and Aue, 2). On the other hand, long periods of rain may prevent the formation of a large aphid population (Steudel, 65, and Broadbent, Chaudhuri and Kapica, 12), or strengthen the effects of attacks by parasites.

3. The influence of wind conditions

Davies (20) studied the effect of wind on the flight activity of 25 winged *M. persicae* placed in a glass wind tunnel, and noted their reaction at different wind velocities. At 0 km per hour, he observed 155 flights per minute, and 25 at 3·2 km per hour. At a wind velocity of 6 km per hour, there was no flight of aphids although they continued to crawl around in a most lively manner, and it was not until the wind velocity had reached 10·8 km per hour that the aphids were subdued into almost complete inactivity. At much higher wind velocities of 32 to 48 km per hour, the aphids had no difficulty in clinging to the glass wall of the tunnel. These results were later confirmed by Moericke (49), Müller (55) and Ziegler (78 and 79) in field studies. It is, therefore, evident that the aphids can only fly during a lull or when a slight wind is blowing, whereas in stronger wind conditions they are forced to remain on the plants and wait for a favourable opportunity to take off. Once they have flown from their host, they may be caught up in strong winds and carried over long distances, extending sometimes for even several hundred kilometres. For example, swarms of *Delachnus piceae* are reported to have appeared in the Spitzbergen Islands, their next nearest plant hosts being on the Kola peninsula some 1300 kilometres away (Davies, 20). Such cases are of course exceptions. Generally, it needs no more than a light wind to carry aphids over distances of a few kilometres. This explains why in summer relatively numerous green peach aphids appear in districts where few possibilities are offered for overwintering (Moericke, inter alia). In this, upward currents which carry the aphids after they have taken off, constitute a factor of considerable importance. According to Ziegler (79), the distance covered by the aphids depends upon the altitude they reach after their start. Thermal upcurrents are

expected to prevail chiefly in depressions and basins, in other words in protected places, and it is here that large aphid populations are mainly found. The type of soil is also an influential factor. In moorland and sandy areas, high temperatures often prevail on the ground surface, and these are favourable to the formation of upward currents. Furthermore, dynamic upcurrents are also caused when horizontal air currents strike a hill or mountain.

Just like the thermal upcurrents, the dynamic upcurrents also assist the take-off and continued flight of aphids provided they do not happen to become caught in an eddy. Such upcurrents and turbulence are of importance especially in hilly districts, the air circulation, therefore, being greatly modified by the relief of the surrounding country. With respect to thermal upcurrents and their importance to the flight of aphids, Ziegler draws a distinction between two stages of air stratification:

1. In fine weather, boisterous upcurrents prevail because the lower air layers are warm and the upper layers are cold. These upcurrents provide good possibilities for the aphids to take off and spread. Consequently the aphids can reach high altitudes and thus be carried over long distances. In view of this, Gersdorf (25) also concludes that in most years the change in population density of *M. persicae* in North Germany cannot be traced back to the intensity of oviposition on primary hosts or even to their number.
2. In bad weather, the position is reversed with regard to the air layers, so that the possibilities for take-off and spread of aphids are greatly limited. In this case, they can only be carried over short distances by horizontal winds.

In exposed potato stands, i. e. in degenerated or young stands or in those full of gaps, the prevailing air conditions are similar to those in fine weather, so that the aphids have good opportunities for flying off. For this reason, heavily degenerated stands are particularly dangerous as sources of infection, especially on fine days. In compact stands, on the other hand, the air layer is cooler (static layer), so that the aphids can only take off from the top leaves.

Hansen (29) made a close study of the effect wind protection has on infection. In the tests he conducted, he arranged for one plot with and one without wind protection at each test location. The results obtained in 30 tests showed that on the average the degree of infection in the plots protected against wind was approximately 27 % higher than in the unprotected plots, although considerable differences were established as shown in the following table:

	Average degree of infection (Y)	Ratios for Degree of infection with : without wind protection	Ratios for Max. aphid population with : without wind protection
Degenerated fields	51 %	109 : 100	118 : 100
Fields of medium infection	25 %	167 : 100	144 : 100
Seed potato fields	6·5 %	76 : 100	560 : 100

This means that the aphids spread out in degenerated areas without much regard for wind protection in the stand, but in places where the conditions for their development are less favourable, they remain in the shelter of hedges, woods etc. This is applicable especially in marked healthy areas where, according to Hansen, the purely mechanical transmission is a factor of relatively great importance in addition to transmission by aphids.

On the other hand, isolated fields which, for example, are surrounded by wood, or isolated potato plants growing in grainfields are by no means protected against a high rate of infestation (Moericke, 49, and Profft, 55). Davies and Whitehead (22) report that isolated potato plants growing in beet or mangel fields were all colonized, even though the adjacent plants were not affected.

Concerning the effect of the different climatic factors, it should be mentioned that in the end the microclimate prevailing in the stand has a considerable influence. With regard to temperature and relative humidity, there are often appreciable differences between the climate in the stand, particularly in a compact stand, and the macroclimate.

4. The influence of the plant's state of health

Heinze and Profft (34) presume that during the course of the summer, owing to the increased incidence of virus diseases and the resultant inhibition of potato plant growth, there is less food available for the aphids so that their vitality is weakened. Czerwinski (17) observed a relatively large number of nymphs on badly diseased plants, and presumed that special factors brought about by the state of health or the material structure of the plant, had an influence upon the ratio of winged to wingless aphids. Perhaps a lack of food leads to a greater development of winged aphids. On the other hand, Arenz (1) found that the aphids thrived better on potato plants of the "Ackersegen" variety infected by leaf roll, and that they reproduced more and lived longer on these plants than on healthy ones. In explanation of this discrepancy, Arenz states that in plants infected by leaf roll, the translocation of assimilates from the leaves is disturbed so that aphids have sufficient food, whereas they starve on healthy plants of the "Ackersegen" variety. In addition to the fact that virus-infected plants are in themselves a danger to the stand, they are in many cases very heavily colonized by aphids. This is also confirmed by other authors.

According to Kassanis (38), the efficacy of vectors also depends upon whether these fly from freshly infected plants. If so, the symptoms appear later and are weaker than when the aphids collect their virus from plants which have been diseased for some time. In all probability, the virus concentration in the latter is appreciably higher than in newly infected plants.

5. The influence of the planting date

The date on which potatoes are planted out must be considered as an influential factor from two aspects:

1. It determines the date of emergence and, consequently, also the date when colonization is likely to begin. Should the crop emerge at a time when the migrants have not yet appeared, or immediately following the

swarm flight of migrants from the peach trees before winged aphids have developed to any real extent on the summer hosts, then the plants may remain for a time uncolonized (high locations). This, however, is not the case when the date of emergence coincides with the date when the green peach aphids migrate.

2. The planting date determines the stage of growth reached by plants at the time aphids make their attacks and, consequently, the susceptibility of the plants to virus diseases. According to Oortwijn Botjes (cited in 60) — and this has already been pointed out — young plants are more susceptible to viruses than old ones. Furthermore, the vectors become infective more easily on young plants (Bawden, 3).

The aphid infestation depends mainly upon the time when the potatoes emerge, and whether and in what numbers the aphids fly at this time, and also when they appear in the stand after the plants emerge. This explains why several authors discovered a greater degree of infestation in early planted fields than in those where the potatoes were set late on in the season, and why others, in contrast, arrived at results which were just the reverse.

Aue (2) and Koch (41) established in variety trials that earlies were as a rule infested more seriously than middle-earlies or late varieties. Heinze and Profft (34) found that the infestation was much greater on potatoes germinated before planting than on those planted at exactly the same time but which had not been pregerminated. Their explanation for this is that attacks on both groups started immediately after emergence, and that the aphids had one week extra in which to develop on those potatoes germinated before they were planted out.

Similar observations were made by Broadbent, Gregory and Tinsley (14). According to these authors, potatoes planted out early were more seriously infected than those set late, because following the emergence of the early potatoes the flying activities of the aphids were relatively greater than later in the season, and therefore most of the infections were caused in May and June (1949):

Planting Date	March 3	April 20	May 10	May 30
Degree of infection				
Leaf roll	20 %	15 %	15 %	10 %
Streak	29 %	30 %	28 %	21 %

Heinze and Profft (34), Czerwinski (17) and Profft (59) also obtained results of a similar nature when they compared crops which were set at the usual time of the year with those planted out fairly late, and which did not emerge until during June and July. In Profft's tests, however, it was found that the late potatoes were in certain cases far more seriously infected than those planted at the normal time, the chief disease here being leaf roll. According to Czerwinski, crops planted late are attacked by aphids flying from plants set at the usual time. These aphids are already infective, and it appears

that a relatively large number of winged aphids develop on diseased plants growing in older stands. In explanation of the heavy infestation in early planted fields, Nowak (56) states that the aphids are not able to reproduce properly until the growth of the plants advances. As the growth of potatoes in early planted fields is completed first, they are attacked earlier and on a much larger scale.

In contrast, Broadbent, Gregory and Tinsley (14) did not discover any differences of real note among fields planted at varying times, either in the degree of aphid infestation or in the severity of infection. They carried out their tests in 1948.

On the other hand Moericke (49) found considerably more aphids and a far higher degree of infection in potato fields which had been set late. Steudel (65), inter alia, made the same discovery in beet fields which had also been planted late. It is likely that optical factors are partly responsible for this (Moericke, 51 and 52). The light overall colour of late seed growing in rows which have not yet closed up, appears to be a source of particular attraction to aphids. Müller (55), however, states that the more serious infestation of fields planted late is due to the fact that the attacking aphids can spread out better in open than in compact stands.

6. The influence of the variety

It is often found even under otherwise similar conditions, that the degree of infestation by aphids and infection by virus diseases varies considerably among different varieties. Details are given below to indicate how aphid infestation fluctuates on different varieties (according to Aue, 2, Koch, 41. Moericke, 49, and Völk and Hauschild, 73):

a) Earlies

seriously infested: Frühbote, Sieglinde varieties;
infestation of moderate severity: Oberarnbacher, Vera. Frühmölle varieties.

b) Middle-earlies

serious: Toni, Flava;
moderate: Olympia;
moderate to serious: Bona;
weak to moderate: Böhms Mittelfrühe.

c) Middle-late and late varieties

serious: Ostbote;
moderate to serious: Voran;
moderate to weak: Aquila;
weak: Merkur, Ackersegen, Heida, Capella.

The results vary of course under different conditions, and it is for this reason that a generally valid classification cannot be drawn up for the infestation of the different varieties.

Quite a number of reasons are given for the differences in colonization and in the degree of infection. According to Bawden and Kassanis (4), the virus concentration in the different varieties is very dissimilar, which explains the differences in their value as infectors, i. e. aphids become infective more quickly on some varieties than on others. It appears, therefore, that the

virus is more readily accessible to the vectors on certain varieties. In this, the degree of resistance of the variety involved to aphids or virus infections is apparently a factor of no importance. For example, the English variety "Arran Banner" is attacked relatively little by aphids but, on the other hand, it develops a high virus concentration, and is thus a suitable infector for the aphids.

According to Bode (6), the varying degree of susceptibility of the different varieties to degeneration diseases may be due to varying resistance either to aphids or to the virus itself. Furthermore, Bode mentions the tolerance of a variety to the virus, but this factor has hardly any bearing upon transmission.

What is the reason for the difference in the susceptibility of the many varieties to aphids? Koch (41) assumed at first that due to the varying type of the different varieties (stem type, leaf type), a varying microclimate prevails in the stand, but he was unable to confirm this theory because he did not establish any marked differences in temperature and relative humidity. The varieties also differ very little from the morphological aspect (leaf structure and thickness of cuticle). This leaves only physiological reasons which may be held responsible for the varying degree of infestation. Völk and Hauschild (73) also observed that the development of the larvae differed most considerably under otherwise like conditions. Arenz (1) explains the low colonization of the "Ackersegen" variety, in particular, as being due to the fact that the aphids have insufficient food on this variety. He observed that aphids placed on cut-off leaves in Petri dishes were able to reproduce very much better than on normal plants where there was a rapid drop in colonization due to a high rate of mortality. Apparently this is due to a lack of food and not to the action of substances which have a toxic effect on the insects.

Furthermore, the resistance of the different varieties to the virus itself is an important factor. According to Köhler, Bode and Hauschild (42), the resistance to infection of several varieties is as follows: very high for "Aquila", rather high for "Heida", low for "Voran", and very slight for "Ostbote". The rates of infection established in the following crop also corresponded to the above degree of resistance for these different varieties, being 14, 33, 65 and 85 %, respectively. These data also agree with those given above for the varying rates of aphid infestation. It is most conceivable that aphids thrive well and reproduce accordingly also on varieties which are extremely resistant to virus.

7. The influence of manuring

Manuring also has a certain bearing upon aphid infestation and virus transmission, in just the same way as the varieties. Apparently, unbalanced applications of potash or nitrogenous fertilizer have an unfavourable effect, but not phosphorus according to Klapp (39). Manuring with KCl, in particular, reduces the value of potatoes for seed production (Völk, 69, Völk, Bode and Hauschild, 71, etc.). Hofferberth and Orth (cited in 71) at first found that aphid infestation on plants manured with KCl was greater than on plants which had not been given KCl, but this is disputed by the other above-mentioned authors who found very few aphids especially on KCl-manured plants, although they established a very high rate of infection on these plants. Völk, Bode and Hauschild have quoted the following figures in this connection:

	KPN	KN	K	N	O
Mean values for the LTS of *M. persicae*	1800	1680	1190	1660	1590
Mean values for the total percentage of diseased plants	51	46	43	35	27

LTS = daily sum total of aphids; O = not manured.

In the application of the 40 % potash salt, the Cl ion appears to have a specific effect. Völk and Bode (72) only established slight differences between the KCl and NaCl plots with respect to aphid infestation and infection by Y and A viruses; on the other hand, the plants manured with KCl were more seriously infected by leaf roll than the potatoes manured with NaCl. The degree of infection and, in certain cases, the rate of aphid infestation are, however, greater in all plots manured with potash — in other words also those which were manured in addition with nitrogen or phosphorus, or both — and likewise in the plots fertilized with K_2SO_4 than on plants not treated with potash.

According to Völk, Bode and Hauschild (71), the low rate of aphid colonization on potatoes only manured with potash is due to the poor possibilities which the larvae are offered for development, while on the other hand, the high degree on infection is brought about by the fact that the winged aphids are less sedentary — perhaps because the feeding conditions are unsatisfactory — and change their feeding grounds more frequently with the result that they transmit more virus. It is, however, probable that these differences are due to physiological and morphological changes in the plant, which influence firstly the relationship between host and insect, and secondly the relationship between host and virus. Bode (7) states that potato plants manured with potash contain more water and chlorophyll than plants lacking in potash; furthermore, the diameter of their epidermis and the diameter of the chlorophyll layer below the epidermis are increased, the corners of the collenchyma cells are thickened and the cells of the cortex parenchyma are enlarged. These changes impair the feeding conditions for the aphids, and it is also probable that the flavour is affected. The above-mentioned effects of potassium chloride also lead to a change in the disposition of the plant towards the virus. The influence which this change has upon the uptake, translocation and reproduction of the virus is unknown according to Völk and Bode (72).

Krüger (cited in 72) and Broadbent, Gregory and Tinsley (14) found that there was an increase in both aphid colonization and virus infection when the plants were given a large dosage of nitrogenous fertilizer. According to Krüger, the rapid and luxuriant growth of the plants after being manured with nitrogen, stimulates the development of the vectors, the stand soon closes, and the plant dies off later. This favours reproduction, on the one hand, and migration from plant to plant, on the other hand, whereby fluctuating virus transmission is also stimulated. Nitrogen manuring, therefore, changes the disposition of the plant to the vector, but it also has physiological effects, namely increased content of glucose, speedier dissolution of reserve

substances, increased respiration, greater exchange of nitrogen compounds, increased growth, and a softer and more succulent tissue, so that probably the resistance of the plant to infection is also reduced.

According to Kassanis (38), the nitrogen dosage also influences the infectiveness of the plant in respect of leaf roll virus. It was observed that aphids became infective more slowly on potatoes manured with nitrogen than on unfertilized potatoes, although they fed longer and reproduced better on the fertilized plants. Kassanis attributes this effect to a lower virus content of those plants which were manured with nitrogen.

The other two main nutritive substances, phosphorus and calcium, apparently have no influence upon virus transmission by aphids, or if so then only to a very slight extent. According to Arenz (1), the influence of the state of health of the plant and of the variety is generally more important than the influence of manuring. Furthermore, manuring is carried out at all events on the average farm, and according to Klapp (39) nutritive substances like chlorine-free sulphates, which physiologically are particularly suitable for potatoes, do not appear to have a favourable influence, i. e. which is evident, on the incidence of virus diseases. On the other hand, there are always certain possibilities for selection with respect to variety and planting time.

IV. The special relations between the vectors and the incidence of virus diseases

The activity of the aphids, the time and extent of their occurrence, and their ability to transmit viruses are all factors which have a bearing upon the degree of infection by virus diseases.

1. Relationship between the extent of vector infestation and the degree of infection

A high rate of colonization is in most cases followed by a high degree of infection although this relationship cannot be expressed in definite figures. On the other hand, a low rate of colonization is not always coupled with low percentages of infection. It is, therefore, hardly possible to draw conclusions from the extent of infestation as to the rate of virus infection, especially when a comparison is made of different locations and years. According to Köhler (cited in 35), the degree of infection is a function of the activity of virus-transmitting aphids, provided that sufficient infectors are present. Rönnebeck (60) states that genuine relations exist at all events at the same location and in the same year. On the basis of tests he carried out in Wales, Davies (18) grouped the potato growing areas in that country into districts suitable for seed potato production and degeneration districts. In the former, the peak of *M. persicae* infestation did not rise above 20, and in the latter it did not drop below 100. This grouping, however, is of little significance because according to Broadbent and Gregory (13) and Doncaster and Gregory (23), infestation in seed potato production districts in other parts of England may well exceed the given peak of 20 in many a year. Heinze and Profft (33 and 34) state the same for Germany. Hansen (29) established in Denmark that aphid numbers and rates of infection may correspond well within a district, but his results were obtained over a space of only two years, and cannot therefore be applied generally.

A number of authors found no fixed relations between the extent of vector infestation and the degree of infection. Hey (35) recorded the same degree of infection at different places in the Soviet Zone (1949 crop) but established the following maximum infestation: 390 *M. persicae* and 1163 other aphid species in Berlin; at other locations: 6 and 20, 14 and 9, 2 and 13; one year later he established that an infection of 56 % corresponded to a maximum infestation of 5 *M. persicae* and 15 other aphid species, while an infection of 10 % at another location corresponded to an occurrence of 4 *M. persicae* and 27 other aphid species. A similar disproportion is quoted by Broadbent and Gregory (13):

		Degree of infection by *M. persicae*		
		Rugose mosaic	Leaf roll	max. per 100 leaves
1945:	Rothamsted	5·4	18·4	111
	Sutton Bonington	1·2	14·2	8000
1946:	Rothamsted	8·5	17·2	77
	Sutton Bonington	11·6	13·7	952

Tests conducted by Aue (2), Doncaster and Gregory (23), Schreier (64) and others produced similar results. This means that according to these findings, there are no proportional relations between aphid numbers and the spread of virus.

2. The bearing of different aphid forms upon the transmission of viruses

There are fundamental differences in this respect between winged and wingless aphids. Furthermore, a distinction has to be made between winged spring aphids and winged summer aphids. The winged forms occurring in autumn are regarded as having no bearing upon the transmission of viruses on potatoes.

The migrants are to be considered as free from virus when they reach the potato fields after their swarm flight. Davies and Whitehead (21) counted only 4 virus infected potato plants among a total of 81 which were colonized by migrants immediately following the first flight and were then protected against further infections. Doncaster and Gregory (23) are of the opinion that, following their swarm flight, the migrants perform the transmissions of virus when they make their frequent, short colonizing flights in the potato field. As the young potato plants are still very susceptible to infections at this time, the above authors believe that the migrants have a much greater bearing upon the infection of the field than the apterous and alate virginogeniae which develop later. The remarks of Davies and Whitehead (22) concerning the importance of colonizing flights show that they agree more or less with the statement of Doncaster and Gregory. Moericke (49) on the other hand, is of the opinion that the alate and apterous aphids occurring in high summer have a much greater bearing upon the

transmissions of virus because their population is 100 to 1000 times bigger in numbers than that of the migrants occurring in spring.

The situation is somewhat different regarding the importance of spring alate aphids when they are of virginogeneous origin, which is chiefly the case in England. They may carry potato viruses from cellars, pregerminating houses, greenhouses or from plants, and cause virus transmissions immediately they fly into a field.

Opinions differ on the extent to which summer alate aphids are responsible for the virus infection of a field. Broadbent and Tinsley (16) report that 83 % of infections by Y-virus and 97 % of leaf roll infections were caused by aphids, as established in tests they conducted, although these results were obtained at a time when there was a very high initial infection. According to the above authors, the apterous aphids spread the virus merely from stem to stem among the different plants.

When the alate aphids have already become infective in the larval stage while developing on their host plants, they are capable of spreading the virus over large distances during their swarm flights in summer. It should, however, be noted that by this time the plants are already very resistant to infection. Oortwijn Botjes (cited in 60) found that the vectors become infective readily on young plants, and also re-infest such plants more easily. The efficacy of the vectors appears to be greatest in May and June.

It must, therefore, be assumed that transmission by apterous aphids takes place in June because at this time of the year the wingless offspring of the migrants are present in the fields in far greater numbers than the migrants themselves. When they migrate, the wingless aphids take the direct route from one plant to the next by crawling across the leaves in preference to the more round-about and troublesome way along the ground. It is, therefore, easier for them to migrate to plants in one and the same row than to plants in adjacent rows. Czerwinski (17) studied this migration of apterous aphids by staining 1200 of them on one plant. Next day he counted 53 % of all aphids which had migrated (about 200) on plants adjacent to the original host, and 9 % on the next two plants of the same row, which meant that 62 % of all migrated aphids remained in the original row while 35 % moved on to the two adjacent rows. Of these, only 3 % were found in rows farther away. Although the very early infection of adjacent plants and rows and the presence of "infection nests" was observed some time ago, no general opinion has yet been expressed as to what extent alate and apterous aphids are responsible as individual groups for the transmission of potato viruses. Apart from the purely numerical proportion of both forms, the type of weather prevailing during the vegetation period with its influence on the reproduction and agility of the vectors, most certainly has a great bearing on transmission.

3. The spread of virus infections in potato stands

The differences in the rate of aphid infestation within one field are often very considerable, and in fact infestation may vary greatly from plant to plant even in conditions which appear to be identical. According to Kunze (45), the reasons for this are still unclear. A possible explanation may be the varying

rate of reproduction due to the dissimilar microclimate or the unequal nutritive value of each plant (Moericke).

An increase in aphid infestation and virus infection, however, is often observed towards the periphery of the field. It is difficult to offer a general explanation for this, too. Müller (55) is of the opinion that increased infestation at the edges of fields may be attributed to the behaviour of the aphids during their colonizing flight. He states that the flying insects resemble a dense cloud which glides over the ground. When this "cloud" strikes an obstacle (plants), it depends upon the density and compactness of the obstacle as to what happens. In incompact stands, the swarm flies on undisturbed and settles among the rows of plants in a uniform manner. When the stand is compact, the swarm does not pass over the plants but ebbs against the plants at the periphery or flies away along the side. Müller believes this to be the reason for greater infestation at the periphery of fields, and concludes that the aphids are practically unable to reach the plants growing in the middle of the stand. Apparently these are colonized later by aphids attacking from the plants on which they have settled at the periphery.

A focus of infection develops in a healthy potato field when one infective alate aphid migrates into the stand, and then flies from plant to plant depositing larvae, and at the same time transmitting virus. This "saltatory" transmission (according to Rönnebeck) is followed by the "fluctuating" transmission, i. e. spread of virus by apterous aphids which have developed in the meantime. According to de Jong (cited in 49), the aphids are compelled to migrate when the host plant dies, or when for some reason or other the aphids are no longer able to pursue their normal activities on this plant. This raises the question as to the distances over which viruses are spread by means of this fluctuating form of transmission. Davies (cited in 49) established that apterous aphids can cover a distance of up to 5·6 metres a day. When they migrate perpendicularly to the direction of the row, however, they seldom cover a distance of more than two rows, according to Czerwinski (17).

Apparently they have difficulty in crossing the ridges. It would seem that the aphids are not very firmly settled on a leaf so that they may easily be knocked off, and carried to other parts during cultivation work or by strong winds (Czerwinski, 17, Profft, 58). The following results give an indication of the bearing which the migration of apterous green peach aphids may have upon infection:

Murphy and Wortley (cited in 43) carried out a series of 9 tests in which a row of plants completely diseased by leaf roll served as infectors. In the row immediately adjacent to the infectors, the authors found that 14 % of the plants were infected by leaf roll, with 5·5 % in the second row, 3·5 % in the third row, and 2·7 % in the fourth row.

Hansen (29) found in tests he carried out, that in the first row next to a row fully diseased by rugose mosaic, 32 % of the plants were infected, and 21 % in the second row.

Similar findings are also reported by Czerwinski (17). Doncaster and Gregory (23) established that new infections accumulate around virus-diseased plants, so that there is a genuine relationship between the development of a new infection and the infector plants.

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On the Epidemiology and Control of Leaf Roll on Potatoes

By Wolfgang Rönnebeck

I. Introduction

Oortwijn Botjes (1920) made a most important discovery when he found that leaf roll can be transmitted by aphids. In fact this discovery was so surprising and completely new at the time that it was not recognized at first in Germany, although from 1925 to 1929 Opitz (1930) carried out tests to check the virus theory of Quanjer by making use of gauze hoods, and in the course of this series, especially among the progeny plants of the 1927 tests, he recorded yield increases of 70 % and 45 % for those plants grown under gauze. Twenty to twenty-five years ago, German scientists studied and confirmed the views which meanwhile had become widespread in Holland and the English-speaking countries, so that it was natural for the spread of leaf roll virus to be regarded as being dependent upon the number of green peach aphids present (*Myzus persicae* Sulzer). This view was strengthened by the fact that in Eastern Germany, especially in Pomerania and East Prussia where the green peach aphid rarely occurred, the potatoes remained healthy for lengthy periods, whereas in the vicinity of Berlin and in Rhineland where it was known from experience that a potato crop was rapidly infected by leaf roll, these aphids were very often found on potatoes in June and July (Heinze and Profft, 1939). It was most clearly established that there was a relationship between incidence and the climate of the locality, and it was believed that in the num-

ber of peach trees, the main winter hosts of *M. persicae,* growing in a region, a factor determining the increase of leaf roll had in the end been found.

Considered generally, and particularly in extreme cases, this is without doubt correct. But the more one studied the finer points of the conditions, less confirmation was found of a relationship between leaf roll infection and the scale of increasing *M. persicae* infestation. Special reference to this has been made by Broadbent and Gregory (1948). Their results prove that a cogent relationship between the infection and the number of vectors does not exist, and therefore that every forecast based solely on aphid counts would be completely dubious.

II. Formulation of the Problem

Instructive facts on the epidemiology of leaf roll were obtained in tests conducted to prevent the spread of leaf roll virus by applying modern, highly effective insecticides belonging to the group of phosphoric esters (Rönnebeck 1950, 1952, 1954, 1955).

In these tests, the preparations used ("E 605", "Systox") were applied in high dosages so that the aphid population was eradicated quickly and completely.

Consequently, infections could only be caused in sprayed plots

1. by alate aphids,
2. before the spray series was started.

When the tests were commenced, no thought whatsoever was given to the second possibility because it was definitely assumed that no infections would occur as long as

a) no *M. persicae* were found and
b) the plants had not grown to the stage where they touch.

In 1947, there was such a big summer flight that the failure of the control measures could easily be attributed to this. It could not be established later to what extent infections had already been caused before the first spray was carried out.

The 1948 test proceeded quite differently, however. The plants in the test plots emerged about the middle of May. They were not given the first spray until June 2 because rain held up the work and furthermore the plants grew so slowly that they were only about 10 to 15 centimetres tall on the above date so that there were still gaps between the foliage of each plant. The infestation of *M. persicae* had increased to an average of 2 aphids per leaf (200 per 100 leaves). During the third part of June, marked primary effects of leaf roll were evident on the Erdgold and Voran varieties. The count taken on June 26 showed that incidence was equally widespread in both treated and sprayed plots. This condition changed, however, during the following period. The check carried out on July 15 showed a most varying increase in both groups of plots, which was also confirmed by the count on July 27.

The recorded values are plotted in Fig. 1 as a percentage of the final infection (primary effects). This curve, allowing for the (assumed) incubation period of one month, is compared with rapidly increasing *M. persicae* infestation (maximum infestation = 100).

With respect to the question raised here, the 1948 test revealed that

1. the transmissions of leaf roll virus apparently begin very early and that
2. they are more frequent around this time than might be assumed from the number of vectors.

A tentative test carried out in 1950 when there was a minimum infestation of potatoes by *M. persicae* (maximum 8 to 12 per 100 leaves), showed that infections are caused even under such conditions. It was quite evident here that the plants adjoining the secondary-infected plants (not removed) had caught far more infections than those plants growing somewhat farther away.

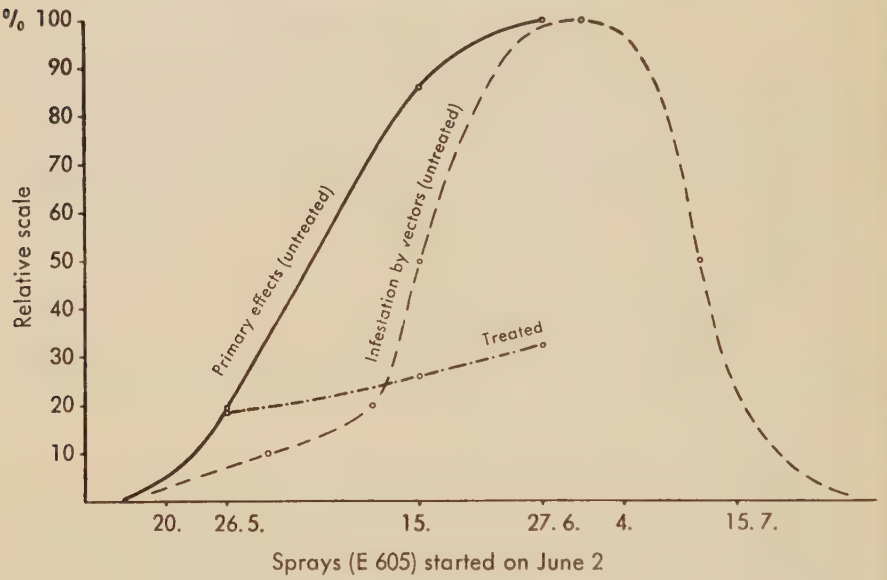

Fig. 1: Increase of primary infections (leaf roll) on Erdgold and Voran varieties in relation to control of vectors (Poppelsdorf, 1948)

From these tests and several studies conducted, conclusions were drawn which at that time were rather venturesome (Rönnebeck, 1952):

1. The result of aphid counts is of secondary importance when estimating the infection.
2. To obtain control of vectors, it is not enough simply to kill the "mass" of aphids where the infestation is mainly concentrated.
3. The slight initial colonization by *M. persicae* in seed production areas before and at the time of roguing results in infections of adjacent plants.
4. A control of vectors must be started very early, when the green peach aphids begin their main flight from the winter host to the summer host (ear formation of winter rye).

5. On the basis of an analysis of conditions in seed production areas, a control of vectors carried out along these lines will have a marked effect on the health of the progeny plants.

This forecast of the effects of vector control in healthy districts was based on deductions. The purpose of the following tests was to check epidemiology and control of leaf roll.

Basically, the following questions had to be clarified:

1. Does a very slight *M. persicae* infestation, so slight that it can hardly, or in fact not at all, be established by means of the 100 leaf method, lead to infections of plants adjoining those already infected?
2. What significance does this process — insofar at it exists — hold for the further infection of the stand?

III. Obtaining Proof of very early Infections

1. Tests conducted in 1952 under conditions approaching those prevailing in the field:

The experience gained is based on two field tests conducted in mountainous districts, and in which the 1st spray was omitted on a part of the area treated. Among the progeny plants, the infection in the plots only given the second or second and third treatments, was compared with that recorded in the plots where the first treatment was also carried out. It was established that as a result of the first treatment which was carried out 12 and 14 days, respectively, after emergence, a high percentage of leaf roll infections was prevented. This percentage amounted to:

	based on all infections caused	based on infections to be prevented by vector control
in Test I	50 %	69 %
in Test II	40 %	48 %

This means that in these tests, 50 % and 40 %, respectively, of all leaf roll infections caused had occurred in the 3rd and 4th week after emergence. Towards the end of the 2nd and 4th week, respectively, after emergence, the *M. persicae* infestation amounted to:

	12th day	4th week after emergence
in Test I	0	10—25/100 leaves
in Test II	0—10	100/100 leaves

The maximum infestation recorded in both tests was approximately 500 per 100 leaves.

When the recorded values are plotted in relative curves (cf. Fig. 2), there is a marked phase shift between the curve for infections and that plotted for

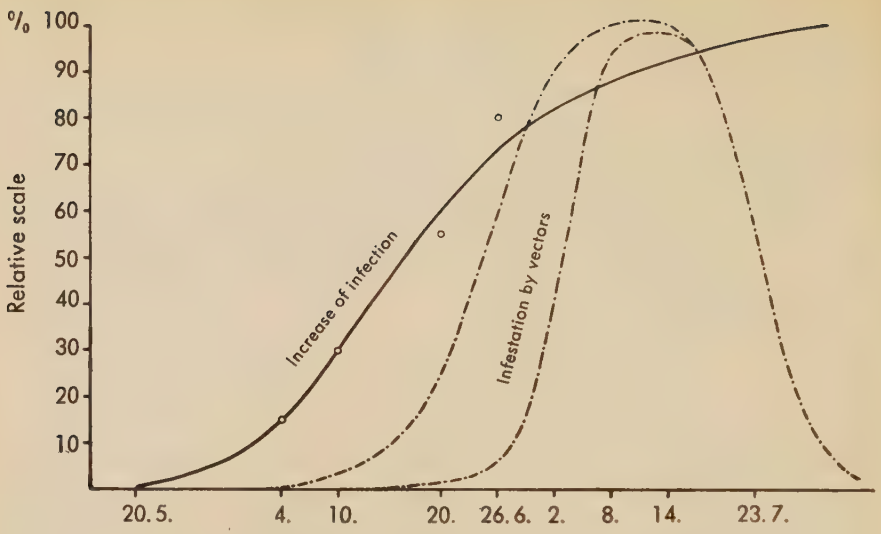

Fig. 2: Relations per unit time between rapidly increasing infestation of *Myzus persicae* and spread of leaf roll virus

M. persicae infestations. The infection curve runs considerably ahead of the infestation curve. This means that the effectiveness of *M. persicae* as the vector of leaf roll virus is considerably greater at the start of colonization than at the time of maximum infestation.

2. Further investigations conducted in the test field of the Institute for Phytopathology, Justus Liebig University, Giessen

The effects of vector control, early picking and selection were compared with each other in order to obtain further information on conditions pertaining to the spread of leaf roll virus. The tests were carried out in 1954 and 1955, both years being characterized by a most varying infestation of potatoes by *M. persicae*. This condition raises the value of the results. In 1954, the test crops (Bona variety) emerged between May 25 and 31, and were immediately colonized during a strong flight of migrants which took place between May 24 and 29. The general plan of the test plot was as follows:

β	β	β	β
α	α	α	α
α	(J)	(J)	α
α	α	α	α
β	β	β	β

J = infector
(secondary leaf roll infection)

a) Selection test

Date of roguing	Percentage of leaf roll on progeny plants	
	α plants	β plants
June 12	33	25
June 19	37	25
July 2	39	32
not rogued	39	40
without infectors	2 %	

b) Harvesting date test (rogued on July 1)
1. without vector control

Harvested on	Percentage of leaf roll on progeny plants	
	α plants	β plants
30. 6. 54	5	2
10. 7. 54	14	6
20. 7. 54	8	6
30. 7. 54	27	8
10. 8. 54	35	19
19. 8. 54	35	23

2. with vector control (on June 4 and 20, 1954)

	at a rate of 1 litre of "Systox" per hectare	
30. 6. 54	0	1
10. 7. 54	1	0
20. 7. 54	0	0
30. 7. 54	2	1
10. 8. 54	6	4

What conclusions are to be drawn from these results?

1. As roguing carried out on June 12, a fortnight after emergence, did not prove very successful, it must be assumed that the first infections on the α plants had been caused beforehand, and that the further infections (fluctuating propagation) spread from these. This provides an explanation why roguing carried out late in the season is not accompanied by an appreciable increase in infection. The initial impulse is no longer needed for fluctuating spread such as encountered here. Therefore,

when several shoots of the α plants growing around the infected plants are also infected, roguing of infectors is no longer of importance.

2. The vector control carried out from June 4 onwards prevented practically every infection of α plants. It is concluded that the first infections occurred after the 4th but before June 12th. At this time, the first wingless generation on the potatoes had not yet fully developed.
3. The harvesting date tests show that even on June 30, at the beginning of the bloom, leaf roll virus had already penetrated into the tubers, in other words infections must have already been caused in the first half of June. This confirms practical experience that although early harvests greatly reduce infection, they do not suppress it completely because the early harvest constitutes an "expedient", not a genuine prevention of infection. It greatly decreases in effectiveness between July 20 and 30 for α plants and between July 30 and August 10 for β plants, whereas when two vector controls are carried out in the second period there is only a slight increase in infection. It should, however, be considered that *M. persicae* developed in the sprayed area from the beginning of July onwards, and even alate aphids occurred there at the beginning of August. The fact that despite this occurrence there was only a slight infection in this area, indicates that only little virus was carried into the stand from outside and that the sources of infection are to be sought in the stand itself.

The three tests provide together a clear epidemiological picture: Spread of leaf roll virus from secondary-infected plants began between the 6th and 14th day after emergence; roguing carried out later had no appreciable effect. Due to the early start of infections, reduction by means of early picking which in practice was not possible until between July 15 and 20, was moderate, but most considerable following prompt elimination of vectors. Only few infections were carried in from outside the field.

In 1955, *M. persicae* infestation was only very weak. The test potatoes emerged at the end of May and the beginning of June, and the main flight period was during the first ten days of June. Migration, however, was so slight that the first *M. persicae* specimen, a larva in its third stage, was not found until June 16; the maximum rate of infestation was around 25 per 100 leaves.

The test plots were arranged to give 5 rows of high-quality seed (Oberarnbacher Frühe and Ackersegen varities, respectively) on each side, left and right, of a row of infectors. Secondary-infected Oberarnbacher Frühe and healthy plants of the test variety were growing alternately in the infector row itself. As in 1954, vector control was compared with roguing, except that this time roguing and spraying, respectively, were carried out on the same dates which were staggered as follows:

1. June 9
2. June 18
3. July 12

In the test strips where vector control was carried out, all infected plants were left in the rows until harvest, and were marked by means of sticks. In the harvest, the following groups were separated:

a) healthy plants in the row of infectors,

b) healthy plants in the rest of the stand growing next to spontaneous-infected plants in the same row,

c) other healthy plants from the 5 rows on either side of the infector row.

In view of the small numbers of vectors, the plants in group a) gave the clearest result. Due to the high danger of infection (50 % infectors), this result shows what normally takes place in the field as if brought to light under a magnifying glass.

Leaf roll infection in progeny plants, average for Ackersegen and Oberarnbacher Frühe varieties

rogued relative	rogued absolute	from	sprayed absolute	sprayed relative
69	= 49·3 %	June 9	12·5 %	= 17
88	= 63·2 %	June 19	33·5 %	= 46
92	= 66·2 %	July 12	60·0 %	= 83
100	= 72 %	untreated	72 %	= 100

It cannot be established that the 12·5 % infections definitely occurred before June 9. But it is probable that they did, otherwise the roguing carried out on this date ought to have given completely successful results. It is, however, certain that almost 30 % of all infections occurred between June 9 and 19, and an even higher percentage between June 19 and July 12, so that the total infection quota between June 9 and July 12 amounted to 66 %. This means that basically the result is the same as that obtained in the tests carried out in 1952 under conditions approaching those prevailing in the field, and in the 1954 test, although in 1955 there was an extremely slight infestation by *M. persicae:* Transmissions commenced soon after the first migration; marked increase in the infection quota in the second half of June, the 3rd and 4th week after emergence.

A summary is given below of all relative values of the test result:

The absolute infection for untreated plants, which was always rated as 100, was 72 %, 58 % and 20 % for groups a, b and c, respectively.

These values reflect the varying danger of infection for the three groups, arising out of the varying distances of the groups from the infectors.

From this summary, the following points can be deduced:

1. The greatest increase of infections sets in somewhat later among the less exposed plants (b + c) than among those plants exposed to a high risk of infection (a).

Vector control (only on given dates)

	Group designation			
	average	a	b	c
from June 9	18	17	18	18
from June 19	33	46	27	27
from July 12	83	83	85	82
untreated		100		
Roguing				
from June 9	51	69	—	33 *
from June 19	60	88	54	37 *
from July 12	82	92	89	66 *
untreated		100		

* Oberarnbacher Frühe variety only

2. The effects of roguing are much greater in 1955, a year when there was a slight vector infestation, than in 1954.
3. The effect of roguing is much greater among less exposed plants than among those exposed to a greater danger of infection (cf point 1 above).

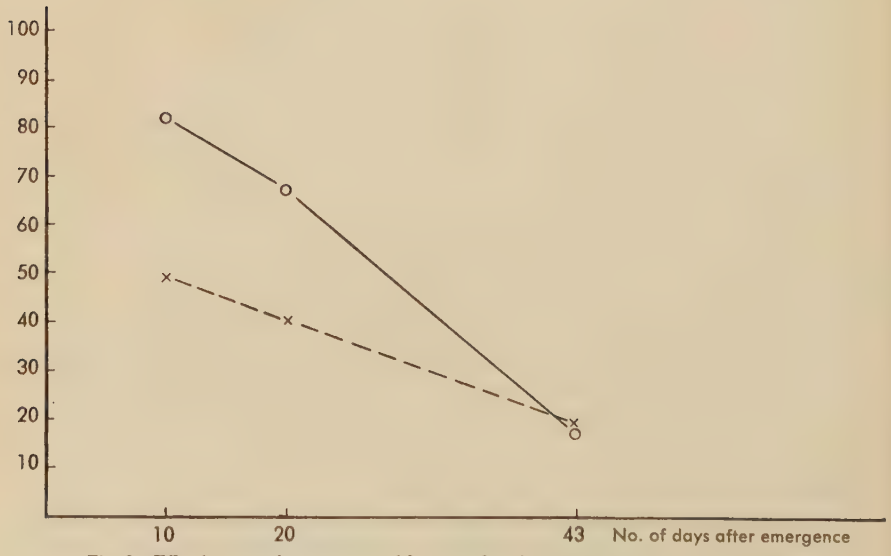

Fig. 3: Effectiveness of vector control [○——○] and roguing [×——×] when starting control measures at various times after emergence (Giessen, 1955)

The effectiveness of a prompt vector control is about the same in both years, and is above 80 % even for plants exposed to the risk of infection. When the start of controls is delayed, the degree of effectiveness decreases very rapidly even when there is only a slight occurrence of vectors (Fig. 3).

IV. Conclusions from the Aspect of Seed Production *

The studies show that the spread of leaf roll virus from secondary-infected plants begins very early in the form of transmissions to isolated shoots of adjoining plants, about 10 to 14 days after emergence. As roguing cannot be carried out so early in the majority of cases because the symptoms of leaf roll are not evident until later, the effect of roguing is not completely adequate. Depending upon the number and activity of the vectors, the susceptibility of the varieties etc., isolated adjacent plants are infected by leaf roll virus before roguing is started — in practice due to shaking off soil and leaving wilting plants lying around for a time also during roguing operations — and to a certain degree these take over epidemiologically the role of the removed plants. The entire process of vector infestation has time to take effect before symptoms of disease appear on the primary-infected plants, which often never happens at all. Geyer, Nicolaisen, also Tamm and Göpp (1935) pointed out as far back as 1935 that an adjacent stand of potatoes infected by virus infects healthy potatoes to a high degree.

Czerwinski (1943) proved that the concentration of infection spreads to only a few rows of the healthy stand, and gave interesting parallels to the results of his tests on aphid migration. Results corresponding fully with these are given in the paper of Doncaster and Gregory (1948) who studied the spread of leaf roll virus and potato Y virus from isolated infected plants. The latter authors also point out that the fact that roguing of infected plants is unsuccessful is not due to the test plots being infected from outside. They give the following proof of this on P. 110: "As usual the new infections of rugose mosaic and leaf roll were concentrated around infected plants already in the crop. In general, ..., the effect of roguing infectors as soon as symptoms can be observed has been negligible." These findings are confirmed by existing results. The effect of the rapidly increasing vector infestation at the end of June and in July is brought about in that the leaf roll virus spreads from the freshly infected shoots and plants. Different stages in the development of this spread of the infection wave were determined when the time for the commencement of vector control was staggered. It should not be imagined that this

* The controls were carried out in 1952, 1954 and 1955 with standard type field sprayers, using a rate of 400 to 600 litres of wash per hectare (1 litre of "Systox" and 1·5 litres of "Metasystox", respectively). The results can be adopted by field workers without any misgivings. The justified reservation with which results are treated that have been obtained with rates of 1000—2000 litres of wash per hectare, with hand sprayers or sprayers fitted with underleaf nozzles, and a rate of several kilos of insecticide per spray and hectare, can be dropped here. Furthermore, the results given prove that when suitable systemic insecticides are applied, complicated types of sprayers and uneconomical quantities of preparation are not needed to control vectors successfully.

"wave" has a definite "front" because, due to the movements of the vectors, isolated infections may be caused rather early also large distances away.

It is certainly not correct that practically all leaf roll infections are already caused before the middle of June, as Doncaster and Gregory conclude (Page 107), simply because roguing carried out on June 19 was unsuccessful. This formulation may be amended today in that the infection waves started to spread from the infectors before the middle of June, and therefore their distance remained ineffective.

Roguing (selection) is without doubt a valuable measure for keeping fields free from infection but it should not be regarded as a measure complete in itself by means of which all infections spreading from secondary-infected plants can be prevented.

Such a view, however, has for many years past led to seed producers attributing "late infections" solely to summer alate aphids. These aphids are of course capable * of causing these infections but there is much evidence to support the belief that infections caused in July are frequently brought about as the result of the wave of infection spreading from secondary-infected plants, at least to a large extent. The wave of infection (fluctuating virus spread) can, however, be suppressed by controlling the vectors. Therefore, in many years it should be possible to prevent "late infections" by corresponding hygienic measures in the field. Seed producers are today faced by the interesting comparison between early picking and vector control; a combination of both methods will give the highest possible degree of virus elimination in the seed.

Practical experience gained with early picking corresponds largely to the reduction attainable by it in comparison tests incorporating vector control. The average virus reduction over a period of five years is recorded at 63 % in the French-speaking sector of Switzerland.

Year	Viruses in %		Reduction in % by early harvesting
	Class B (mature)	Class A	
1951	9·8	3·7	62
1952	38·0	17·2	55
1953	9·5	3·0	68
1954	11·0	2·4	78
1955	7·6	3·6	53
		Five-year average:	63 %

* It is only by means of special tests in which vector control and early picking are carried out separately, that it can be determined in which cases summer alate aphids, through saltatory virus transmission, really play an important part in causing infection.

Schepers, Reestman and Hille Ris Lambers obtained the following results in tests conducted:

			Reduction:
untreated, mature	18 %	infected by leaf roll	
untreated, picked on July 17	6·9 %	dto.	62 %
sprayed 3 times with "Systox", mature	2·6 %	dto.	86 %
sprayed 8 times with "Systox", mature	1·0 %	dto.	95 %
sprayed 3 times with "Systox", picked on July 17	0·3 %	dto.	98 %

The average data for all plants checked in the 1954 test referred to earlier, are directly comparable with these values.

			Reduction:
untreated, mature	23·3 %	infected by leaf roll	
untreated, picked on July 20	6·0 %	dto.	73 %
sprayed twice with "Systox" at a rate of 1 litre per hectare, mature	4·0 %	dto.	82 %
sprayed twice with "Systox" at a rate of 1 litre per hectare, picked on July 20	1·7 %	dto.	92 %

It is evident from these results which, with respect to early picking correspond with practical experience gained, that when virus spread is mainly of the fluctuating form, vector control is clearly superior; the epidemiological principles of vector control have been indicated in this paper.

Summary

The tests conducted to control virus-transmitting aphids provided new information on the epidemiology of the leaf roll virus of potatoes. When allowance is made for this information new possibilities are opened up for controlling this disease.

Tests conducted under practical conditions and in the test field show that transmissions of leaf roll virus begin shortly after a potato crop emerges. It does not necessarily follow that the usual counting methods must disclose the presence of aphids of the *M. persicae* species. Transmissions on shoots of plants adjoining infected plants begin at an earlier date than is possible for carrying out roguing. This practice, however seldom gives a 100 % effectiveness because the wave of infection continues to spread once it has already started. On the other hand, roguing reduces the intensity and distance covered by the wave of infection, to a greater or lesser degree depending of course upon conditions.

The wave of infection, in other words the "fluctuating spread of virus", can however be suppressed by controlling the vectors. In comparison tests carried out, vector control gave greater effectiveness than roguing and early picking.

From these facts, it is concluded that vector control is a most suitable measure for considerably improving hygiene in seed production, and to give roguing that degree of effectiveness expected of it.

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Action of the insecticide "Gusathion" on cotton plants, and the problem of residues in cottonseed

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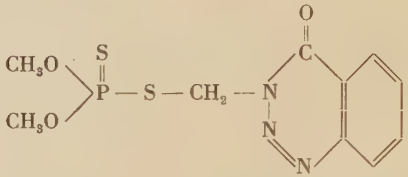
Biological Institute of Messrs. Farbenfabriken Bayer Aktiengesellschaft, Leverkusen-Bayerwerk, Germany.

The insecticide "Gusathion"* or 0,0-dimethyl S-3-(4-ketobenzotriazine)-methyl phosphorodithioate gives effective control of many cotton pests, including pink bollworm, *Pectinophora gossypiella* (Saunders); cotton bollworm, *Heliothis armigera* (Hbn.); cotton bollweevil, *Anthonomis grandis* Bdv.; cotton leafworm, *Alabama argillacea* (Hbn.); cotton aphid, *Aphis gossypii* Glover; red spider mites, *Tetranychus* spp.; and *Thrips* spp., when applied at 0·75 to 1·0 lbs. per A. In as much as cotton is a subtropical culture, infestations by some of these pests continue to occur until the time of harvest. As a result it is necessary to make applications late in the season, sometimes within a few days of harvest, and there is the possibility that several applications may be made directly upon partially opened and unopened bolls. Thus it became essential to demonstrate the nature and magnitude of possible toxic residues in cottonseed oil and cottonseed cake which are used for human and animal foods. Extensive studies were conducted from September to December, 1956, with the object of clarifying this question.

* In the United States registered by the Chemagro Corp., N. Y., as "Guthion", and also known as "Bayer 17 147".

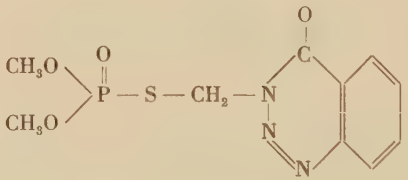
Material and methods

For the purpose of these trials, ^{32}P-labeled "Gusathion" active ingredient with a specific activity of 1·5 mC/g, formulated on October 3, 1956, was kindly supplied by Dr. G. Schrader of the Plant Protection Laboratory of Farbenfabriken Bayer Aktiengesellschaft, Elberfield:



"Gusathion"

On October 16, 1956, the following relative activities were recorded for this compound: 6·94 counts/sec/microgram with the end window counter, and 9·45 counts/sec/microgram with the flow counter. The oxygen analogue P = O "Gusathion" shown below was also supplied by Dr. G. Schrader since the formation of this compound by oxidative metabolism of the P = S to the P = O linkage was anticipated. Metabolic reactions of this type by living systems have been shown to be peculiar to organophosphorus compounds containing dithioate linkages. (March, R. B., et al., 1955; March, R. B., et al, 1957; Metcalf, R. L., and R. B. March, 1953; Myers, D. K., et al., 1952.) Both compounds approximated 100 per cent purity as demonstrated by paper chromatography.



P=O-"Gusathion"

The "Gusathion" active ingredient was formulated as follows:

^{32}P-labeled "Gusathion" active ingredient	= 25 %
Xylene	= 30 %
Dimethylphthalate	= 37 %
Emcol M-500 (emulsifier)	= 8 %

This formulation was applied as a concentrate spray to three rows of cotton, each 9 metres long (30 ft.), at a rate of 32 ounces in 25 gallons of water per acre (= 2240 g/234 l/ha) between October 16 and November 13. A total of 8 sprays were applied at intervals of 4 days, using a pressure-type hand sprayer.

Processing the leaf material

Twenty-five leaves were sampled from each of the three rows thirty minutes after each spraying, homogenized, diluted with water, and counted in parallel tests as a dry assay by means of the Geiger-Müller counter. The recorded radioactivity calculated as intact "Gusathion" active ingredient is given in a table in the section set aside for the discussion of the results (cf. p. 283).

Leaves were sampled from the three cotton rows at different times during the series of applications, and qualitative and quantitative analyses were carried out to establish the presence of toxic residues. Fifty to 100 grams of cotton leaves were first washed twice with acetone. The acetone wash was assayed for radioactivity. The liquid was then evaporated in a Kuderna-Danish evaporative concentrator to dryness. The residue was taken up in 50 ml of chloroform, and partitioned between 50 ml of water. The aqueous layer was then extracted with an equivalent quantity of chloroform. The distribution of radioactivity in the two solvents was determined, and paper chromatographic and microchemical analyses made of the portion soluble in chloroform.

The washed leaves were extracted three times with five times their weight in ethyl alcohol. The leaves, together with the alcohol, were placed in a Waring blendor, and macerated for five minutes, and filtered through a Büchner funnel. The cellulose residue was again poured into the blendor together with alcohol and the procedure was repeated twice more. There was practically no radioactivity in the third filtrate. Following the determination of radioactivity, the combined filtrates were evaporated almost to dryness in vacuum at a water bath temperature of 45 to 60° C, and the remaining residue partitioned between 50 ml of chloroform and 50 ml of water. This was followed by two further chloroform extractions of the water. The water phase contains hydrolysis products such as orthophosphate and the mono and di-esters of the labeled phosphoric acid, products which are no longer toxic, and consequently biologically ineffective. The combined chloroform extracts were evaporated almost to dryness in vacuum at a water bath temperature of 45 to 60° C, and the residue was taken up with 200 to 400 ml of acetone which contained 0.1 % methanolic, saturated $CaCl_2$ solution. Within a period of 24 hours, more than 95 % of the phosphatides and phosphatide acids separated as precipitates and were collected and washed with acetone. The acetone filtrate from the $CaCl_2$ precipitation was concentrated in vacuum, the residue taken up with acetonitrile, and partitioned between petroleum ether saturated with acetonitrile. The major portion of the radioactivity partitioned into acetonitrile, leaving only a trace in the petroleum ether phase together with all the green, and to a large extent the yellow pigments. The acetonitrile phase was concentrated, added to a chromatographic column filled with acid Al_2O_3 and eluted with acetonitrile. The radioactive substance added to the column was eluted in one fraction, and interfering pigments were left behind in the Al_2O_3. The fraction was again concentrated and subjected to paper chromatographic and microchemical analysis. The paper chromatogram was prepared with acetylated paper and a solvent mixture made up of 35 parts of tetrahydrofurane, 6 parts of ethyl acetate and 47 parts of water, according to Micheel (1954). By means of this method, "Gusathion" produces an R_F value of 0.22, whereas P O "Gusathion" gives an R_F value of 0.65.

For the microchemical analysis, the method described by MacDougall (1956) for detecting "Gusathion" residues in cottonseed oil was used. In this method the intact "Gusathion" molecule is hydrolyzed in alkaline solution. The anthranilic acid formed in the process is diazotized, and coupled with N-(1-naphthyl)-ethylene diamine. A strong color complex is formed. The reaction is described in a paper published by Averell and Norris (1948). It should be mentioned that MacDougall succeeded in showing that neither benzazimide (4-keto-3 H-1,2,3-benzotriazine) nor hydroxymethyl-benzazimide (4-keto-3-hydroxymethyl-1,2,3-benzotriazine) formed colored complexes under the same conditions as did "Gusathion". Thus, MacDougall precludes any possibility of decomposition products of "Gusathion" active substance being included in the analysis. Two more leaf analyses were carried out in the same manner as described above, except that this time the leaves were not washed with acetone.

Processing of the seeds

The mature, open bolls were picked separately from each row. Delinting was carried out mechanically. The fibre residues adhering to the seeds were removed with concentrated sulphuric acid. The seeds were washed under running water and then placed in

acetone for a short period to dry. The solvent was removed by spreading the seeds in a drying chamber where they were left for twenty minutes at a temperature of 60 ° C. The seeds were ground in a Wiley mill, and the total radioactivity of the seed meal was determined by wet ashing with concentrated nitric acid.

Preliminary fortification experiments carried out in support of the analysis to determine the presence of toxic residues by adding 0·0182 mg of ^{32}P-labeled "Gusathion" active ingredient to 50 grams of untreated cottonseed meal showed that recoveries of 92—98·5 % were obtained from the meal by two cold extractions with petroleum ether. (The meal is agitated each time for ten minutes with petroleum ether in the Waring blendor, and the petroleum ether is drawn off by suction. In this process the oil is also largely extracted from the meal.)

The "Gusathion" active ingredient was then extracted from the petroleum ether-oil fraction, ratio of 5:1, with an equivalent quantity of acetonitrile saturated with petroleum ether. It was determined that 98·1 % of the radioactivity was extracted into the acetonitrile phase with a single extraction. In view of other sources of errors in the procedure, it may be assumed that "Gusathion" passes over quantitatively into the acetonitrile phase with one extraction. The petroleum ether-oil mixture no longer showed any measurable quantities of radioactivity. However, in order to ensure complete removal of "Gusathion" in the seed analyses, the petroleum ether-oil fractions were extracted three times with equivalent quantities of acetonitrile saturated with petroleum ether.

The cottonseed meal from the treated cotton was extracted either in the cold by stirring it with petroleum ether in a Waring blendor (the liquid was drawn off by suction on a Büchner funnel and the process repeated three times; the filter residue was re-stirred each time with petroleum ether in the blendor), or was extracted with petroleum ether for six hours in a Soxhlet type extractor. The petroleum ether was removed under reduced pressure, the weight of the raw oil content determined, and the phosphatides in the raw oil precipitated as the $CaCl_2$ complex. After removal of the phosphatide-$CaCl_2$ complex by filtration, the acetone was evaporated under reduced pressure at a water bath temperature of 40 ° C to 60 ° C. To the remaining oil was added two volumes of petroleum ether and the resulting solution was extracted three times with equivalent volumes of acetonitrile. The radioactive substance in the acetonitrile was examined microchemically for toxic residues by means of the method worked out by MacDougall (1956).

Experiments and discussion of the results

a) Leaf analysis

The total radioactivity present in the leaves immediately after each application of P^{32} "Gusathion" was determined and calculated as intact "Gusathion". The values for each separate row and the means for all three rows are given below in Table 1. These values represent the total radioactivity present in each case, and are not a measure of toxic substances.

The quantity and nature of the residues from these applications is of practical signifiance both from a pharmacological as well as from a toxicological aspect. Leaves were sampled at various times and analyzed according to the analytical procedure described in the previous section. Four of these analyses were carried out. In the first two, the leaves and surface residues were analyzed separately, whereas in the following two the total quantity of toxic substance was determined. The quantity of toxic substance purified by the method described was determined in the leaf washes and leaf extracts by radioassay and compared with results obtained by the colorimetric method of MacDougall (1956). It was found that the amounts obtained by radioassay fully conformed with those obtained by chemical analyses. The variations between both analytical methods ranged from 2·4 % to 5·8 %. As reported earlier in the section describing experimental methods employed, the chemical analysis responds to the intact molecule, and not hydrolysis products, indi-

Table 1: Radioactivity present following different spray applications, calculated as "Gusathion".

Application	Date	Row 1	Row 2	Row 3	Mean for Row 1—3
		ppm = mg/kg	ppm = mg/kg	ppm = mg/kg	ppm = mg/kg
1	16. 10. 56	44·6	44·2	53·1	47·3
2	20. 10. 56	86·5	102·5	76·6	87·8
3	25. 10. 56	143·1	178·2	158·7	160·0
4	29. 10. 56	122·5	108·8	271·0	167·4
5	2. 11. 56	159·2	266·5	179·2	194·9
6	5. 11. 56	198·0	266·0	298·0	254·0
7	9. 11. 56	243·0	370·0	313·0	308·7
8	13. 11. 56	252·0	330·0	392·0	324·6

cating that the analyzed material is intact "Gusathion", or possibly the compound oxidized at the phosphorus atom, namely the P = O-"Gusathion".

Further evidence on this point is provided by the paper chromatographic analysis. It is evident both from the graphic representation of the paper chromatogram as well as from the radioautograph, that the formation of P = O-"Gusathion" does not occur either on the leaf surface or inside the leaves of cotton plants. In leaf analysis II (see Table 2 and Figs. 1 and 2), only unchanged "Gusathion" active ingredient was present in the leaf washing. On the other hand, the leaf extract shows a peak at the point where "Gusathion" is expected in the chromatogram, but also shows appreciable trailing.

In order to differentiate the trailing in the "Gusathion" peak, since all components in the spot responded to the colorimetric analysis, a radioautograph was prepared from the chromatogram obtained from Analysis IV (extraction of the leaves without a preceding leaf wash). It is shown here (see Fig. 2) that apparently only a small proportion of intact "Gusathion" is present, and the presence of two other compounds is indicated which, although responding to the chemical analysis, are, however, much more lipophilic than "Gusathion", and according to their R_F values cannot be "Gusathion". As the radioautograph could not be evaluated until after the experimental work had been completed because of the time of exposure required, nothing can be said at present about the toxicity of the other two metabolites or regarding the chemical structure of these compounds.

The data in Table 2 show that there is a steady increase of ^{32}P-labeled phosphorus lipides, particularly after most of the applied "Gusathion" had been degraded to hydrolysis products. ^{32}P-assimilation of the hydrolysis products of radioactive phosphorus insecticides in plants has already been observed in other experiments (R. Mühlmann and H. Tietz, 1956) with methyl isosystox. This will be dealt with in greater detail in the next section in the discussion of seed analysis.

Table 2: Percentages of radioactivity present as hydrolysis products, toxic components and assimilated ^{32}phosphorus (latter present as phosphorus lipides).

Stage of processing	I 3 days after 1st application %	II 4 days after 5th application %	III 7 days after 8th application %	IV 16 days after 8th application %
A. Microchemical analysis				
1. Acetone washing of leaves				
a) Chloroform-soluble proportion (toxic)	37·90	52·30	No leaf washing	
b) Water-soluble proportion (non-toxic)	2·68	7·20		
2. Leaf extract				
a) Chloroform-soluble toxic proportion	22·90	4·50	41·55	39·72
b) Water-soluble non-toxic proportion	23·10	19·50	17·53	5·45
c) Phosphatides	0·51	0·31	1·65	14·40
d) Wet-ashed cellulose residue	9·35	15·70	32·20	38·25
e) Loss of radioactivity due to processing	3·56	0·49	7·07	2·18
B. Total toxic proportion (radioactivity, and also chemical analysis)	60·8 = 17·00 ppm	56·8 = 70·00 ppm	41·55 = 91·80 ppm	39·72 19·50 ppm
C. Total radioactivity of a leaf homogenizate of same origin, calculated as "Gusathion"	30·97 ppm	121·00 ppm	233·00 ppm	116·70 ppm

b) Seed analysis

On November 14, 1956, the day after the last application, the ripe and open bolls were sampled and analyzed separately for each row. Sixeen days later more bolls were picked from Row 1 and a comparison can be made between seeds which were in varying stages of development at the time of application. The data in Table 3 show there is good agreement between the values obtained from the "first sampling" in the three rows.

With respect to the age of these seeds, it must be mentioned that at the time of the initial spray, a large number of the bolls were already open in all

three rows, and in the next two weeks practically all the bolls opened. Those bolls which were already open or were in the process of opening should contain fully mature seeds, or seeds which no longer assimilated or if so then only slightly. The plants in Rows II and III had completed their development, produced no new growth, and therefore did not form any more blooms or seeds. The situation in Row I was quite different. Here, the plants were still

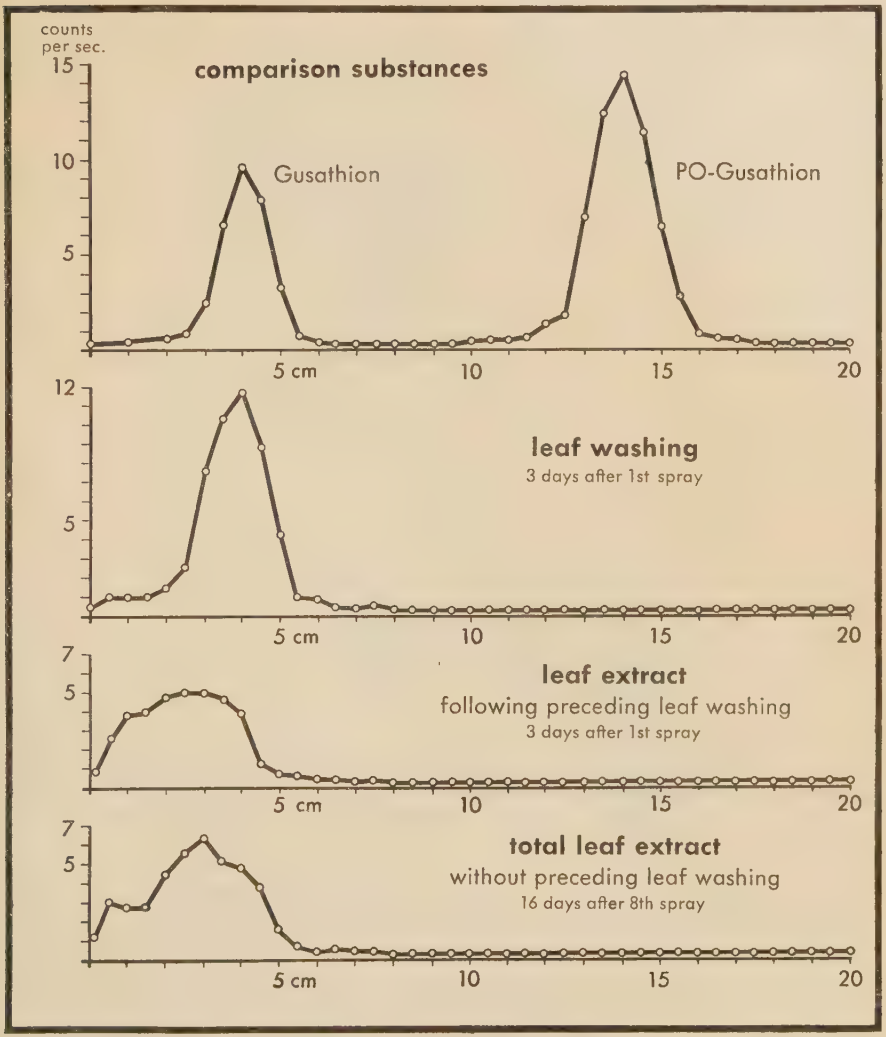


Fig. 1: Graphic representation of paper chromatogram. Analysis of cotton leaves sprayed with ^{32}P-labeled "Gusathion"

growing vigorously during the spray treatment, continued to bloom and form seeds.

At the time of the first picking, there were still large numbers of closed bolls in the top parts of the cotton plants growing in Row I. During the next two weeks, these bolls opened and a second crop was obtained from this row 16 days after the last spray.

Table 3:

	First picking on Nov. 14, 1956			Second picking on Nov. 29, 1956
	Row I	Row II	Row III	Row I
Wet ashing of cotton-seed meal calculated as "Gusathion"	0·516 ppm	0·556 ppm	0·722 ppm	7·58 ppm
Oil yield	17·4 %	17·35 %	14·75 %	21·0 %
Phosphatides calculated as "Gusathion" in oil	0·00442 ppm	0·00420 ppm	0·00647 ppm	0·183 ppm
Acetonitrile extract of oil, possible toxic substance	0·0636 ppm	0·0253 ppm	0·0146 ppm	0·0613 ppm

When the values given in Table 3 for the first and second harvest are compared, a completely different picture is obtained. It will be found that the radioactivity present in the seeds of the second crop is more than ten times greater than that of the first crop. It appears improbable that translocation of the radioactive material through the boll walls or through the dead cotton fibres due to diffusion occurs since the two crops show different quantities of radioactivity. The accumulation of radioactivity in the seeds can, therefore, only have been effected through the conducting bundles, i. e. in the supply of water and assimilates. No other explanation can be offered for the fact that the second crop has more than ten times as much radioactive material as the first crop.

This raises another question, namely whether "Gusathion" acts as a systemic compound in the plant. If so, then it is to be expected that an appreciable quantity of the radioactivity translocated in the seeds still constitutes toxic substance. The leaf analysis at first showed that "Gusathion" is not able to penetrate readily into the green leaf, and neither the surface coating nor the material which penetrates into the leaf is converted into strongly hydrophilic toxic metabolites. Experience gained with systemic insecticides in plant experiments shows, however, that such preparations or their metabolites must be somewhat soluble in water if they are to be translocated in the plant.

In the leaf analysis, the formation of hydrophilic metabolites, e. g. P = O-"Gusathion", was not observed. Therefore, in the seed analysis, care was taken to eliminate any ^{32}P-containing assimilation products which might have been formed from the hydrolyzed preparation. The oil extracted with petroleum ether chiefly contains only lipophilic assimilates in the form of phospholipides. These, however, can be precipitated almost quantitatively with acetone as Ca salts. It should be pointed out that the phosphatides present in the oil in the

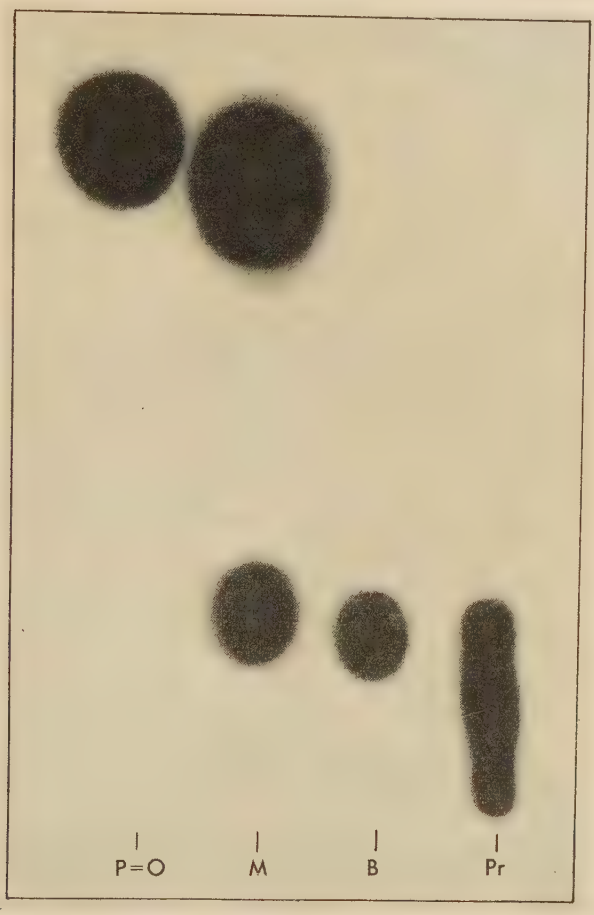


Fig. 2: Autoradiogram of a paper chromatogram. Analysis of cotton leaves sprayed with ^{32}P-labeled "Gusathion". 16 days after the 8th spray.
P=O = P=O-"Gusathion"
M = Mixture of P=O-"Gusathion" and "Gusathion"
B = "Gusathion"
Pr = Plant extract

first harvest showed relatively little ^{32}P-phosphatides whereas in the second harvest this amount increased approximately thirty times greater. Judging from the preliminary analyses, it appears that after precipitation, a toxic substance is present which was extracted from the oil quantitatively with acetonitrile. In fact, traces of radioactivity can be found in the acetonitrile extract of the oil. These quantities range between 0·0146 to 0·0636 ppm, calculated as intact "Gusathion" that might still be present. Such quantities are too small for identification by microchemical or biological assays. However, these quantities are so minute that they would appear to be insignificant in respect to the human consumption of cottonseed oil.

The radioactive residue remaining in the cottonseed meal following the oil extraction is still considerable since a maximum of only 20 % passes into the oil-petroleum ether phase. The radioactive substance left in the meal cannot be intact active ingredient, however, since fortification experiments show that "Gusathion" is extracted to 92—98·5 % by the cold method in two petroleum ether extractions (see page 282). These residues, too, are in all probability assimilated ^{32}P which is present in cottonseeds chiefly in the form of phytin. Reference will be made to this in a later paper.

Summary

1. ^{32}P-labeled "Gusathion" active ingredient formulated as a 25 % preparation, was sprayed on cotton at the rate of 32 ounces in 25 gallons of water per acre between October 16 and November 13, 1956. Eight applications were carried out at intervals of four days.

2. Analyses of the leaves were carried out at four different times using microchemical and paper chromatographic methods. In addition to hydrolysis products which were no longer toxic, unchanged "Gusathion" and two strongly lipophilic metabolites were detected. Apparently P = O-"Gusathion" is not formed. No conclusions could be made regarding the toxicity and chemical nature of the lipophilic metabolites.

3. In addition to the radioactive hydrolysis products, ^{32}phosphorus was also recovered in the assimilation products of the plant, principally in the form of radioactive phosphorus lipides.

4. Seeds which were more or less mature at the time of applications contained only small quantities of ^{32}phosphorus. On the other hand, appreciable quantities of radioactive phosphorus were found in the seeds which were immature at the time of application.

5. Only small quantities of precipitable phosphatides were found in the oil of seeds which were mature at the time of the applications. In contrast, large quantities of ^{32}P-labeled phosphatides were precipitated from the oil of the seeds which were immature at the time of application. In both cases, only slight traces of radioactivity remained in the oil following the phosphatide precipitation, and these were so small that they could not be identified chemically. Therefore, they must be assumed as possible toxic substance.

6. The petroleum ether-extracted meal contains no toxic residues.

7. "Gusathion" does not have appreciable systemic insecticidal action.

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Gall Midges Occurring as Pests on Purple Willows

by E. Scholz-Günther

In the district of the Lower Rhine where osiers are grown, serious damage is caused every year to purple willows (*Salix purpurea* L.) by gall midges.

1. The first larval generation of *Rhabdophaga rosaria* H. Loew which occurred in 1957 about the middle of May, fed on the tips of the rods causing rosette-like structures. The reaction of the plants to this feeding is that the youngest leaves on the rod fold together in the shape of a bag (fig. 1), and dry up after about 8 to 11 days. As a result of the infestation, the rod develops lateral shoots which form from the leaf axils, leading to marked ramification of growth.

   These injuries constitute a serious loss to the grower in that the rods can no longer be used for binding in orchards and vineyards — their main application — but can only be processed as unstripped plaiting material. Consequently the grower has to face a financial decrease in market value amounting to approximately 50 %.

2. Symptoms of attacks by *Rhabdophaga spp.* occurring at the same time on the centre and upper sections of the rods also bring about an additional decrease in the market value of the crop. Nodular galls are formed, and in autumn these burst open as far as the pith of the rod (fig. 2). Holes bored by the larvae (fig. 3) are evident in galls which do not burst open to such a great extent. Compartment-like feeding tunnels filled with larvae are to be found inside the galls (fig. 4).

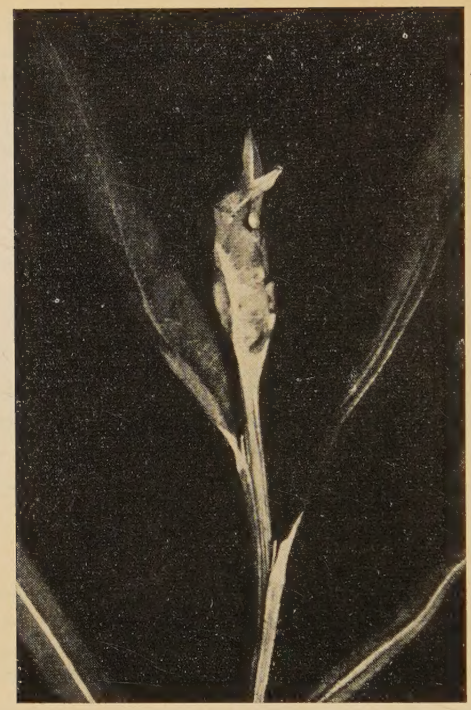

Fig. 1: Bag-like deformation of shoot tip on purple willow, caused by *Rhabdophaga rosaria*

Trial controls of both pests were carried out on May 25, 1957 at Anstel near Rommerskirchen. In these tests, 0·1 % "Dipterex" Emulsion and 0·05 % "Folidol E 605" conc. were applied at a rate of 600 litres per hectare, and each product was sprayed on a plot measuring 1 hectare in area. The rate of infestation at the time of the treatment and the results of the sprays are tabulated below:

	Rh. rosaria	Rh. spp.		Rh. rosaria		Rh. spp.	
Infested rods before treatment on May 25, 1957*	19·4%	8·6%	Number of larvae per symptom following treatment on May 28, 1957**	"Dip-terex"	"E605" conc.	"Dip-terex"	"E605" conc.
				†6·9	5·4	—	—
Number of larvae per symptom**	7·2	1·7		*—	3·1	1·9	2·1

* Average for 4×100 rods
** Average for 4×20 symptoms

These figures show that *Rhabdophaga rosaria* is completely eradicated by "Dipterex" but only partly controlled by "E 605" conc. The latter product is only able to kill the larvae living in the outer layers of leaves. Those larvae present in the inner layers are not completely eradicated.

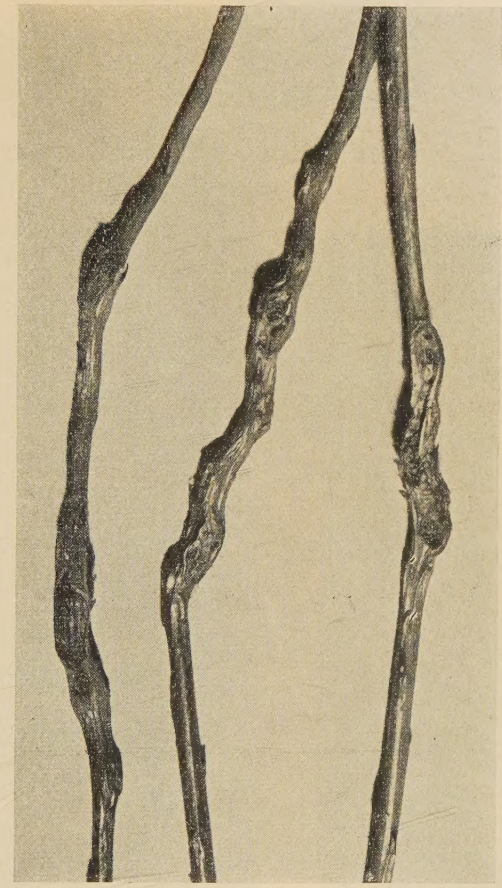

Fig. 2: Formation of galls on *S. purpurea*, caused by *Rhabdophaga spp.*

The larvae of *Rhabdophaga spp.* present in the shoots were not controlled by either product. Aimed sprays of "Dipterex" carried out during the flight period of the imagines (approximately 8—10 days before the treatment was carried out here) should, however, give satisfactory results.

On June 29, 1957, the growers were recommended to carry out a repeated treatment with "Dipterex" to give control of the second larval generation of *Rh. rosaria.*

Fig. 3: Holes bored by larvae of *Rhabdophaga spp.*

Fig. 4: Feeding tunnels and larvae of *Rhabdophaga spp.*